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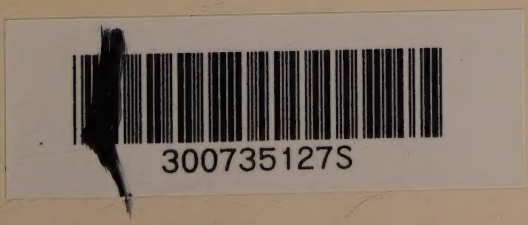

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FIG. 1.—*Lyginodendron Oldhamium.* Restoration. For description see text.

STUDIES

IN

FOSSIL BOTANY

BY

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1909

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PREFACE TO VOLUME II

THE present volume, completing the "Studies," has required an even more drastic revision than Volume I., and is, to a great extent, a new book.

Chapters X. and XI., which deal with the Fern-like Spermophyta (the new class Pteridospermeae) are now written from a fresh point of view, for it is only since the appearance of the first edition that we have become acquainted with the true nature of this extensive group, as shown by its advanced methods of reproduction.

In Chapter XII., now headed "The Cordaitales," the section on the family Pityeae is altogether new, and that on the Poroxyleae considerably extended. Our ideas of the relationships of the groups concerned have advanced greatly, though, as regards the family Cordaiteae, our knowledge still rests essentially on the work of Renault and Grand'Eury.

The Mesozoic Gymnosperms (Chapter XIII.) now appear in quite a new light, owing to the brilliant elucidation of the flowers of the American fossil Cycadophyta by Dr. Wieland, whose work at last

brings the great question of the origin of Angiosperms within the range of scientific discussion.

Lastly, the concluding chapter has necessarily undergone a complete transformation, in order to bring it into harmony with the results of so much new research of fundamental importance. In this chapter a fresh classification of the Vascular Plants has been introduced.

Volume II. contains 36 new figures, from various sources, namely: Figs. 136, 137, 143, 144, 145, 146, 147, 148, 149, 150, 151, 152, 153, 161, 168, 169, 170, 171, 172, 173, 174, 175, 177, 184, 185, 186, 196, 197, 199, 206, 207, 208, 209, 210, 211, 213.

My wife, Mrs. D. H. Scott, F.L.S., has again undertaken the work of preparing the Index.

D. H. SCOTT.

11*th March* 1909.

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STUDIES IN FOSSIL BOTANY

CHAPTER X

PTERIDOSPERMEAE

Lyginodendreae

We now leave the Ferns, and pass on to the Pteridospermeae, a series of forms which are among the most interesting made known to us by fossil botany, for they unite in their organisation the characters of two of the main divisions of the Vegetable Kingdom—the Seed-plants and the Ferns.

It has long been recognised that many of the fronds from the Carboniferous strata, commonly described as those of Ferns, are subject to grave suspicion of not having really belonged to the class Filicineae. Such suspicions attach not only to the so-called genera *Alethopteris* and *Neuropteris*, and to a large part of *Sphenopteris*, but to an actual majority of the Fern-like fronds. The plants in question have never been found with recognisable fructifications of a Fern-type, whereas in the accepted fossil Ferns, specimens with sori occur in a fairly large proportion of cases. It was

on such negative evidence as this (which is not without its value, if drawn from sufficiently numerous instances) that Stur in 1883 based his exclusion of certain of these genera from Ferns and their reference to Cycads. Subsequently, a large body of well-ascertained positive data accumulated, derived mainly from anatomical investigation, on which, indeed, we then had to depend, for in none of the plants concerned were the organs of reproduction known with certainty up to the year 1903. The anatomical characters observed indicated a position intermediate, at least in certain respects, between Ferns and Gymnosperms, the particular class of Gymnosperms approached being that of the Cycadophyta. Hence the convenient name *Cycadofilices* was applied by Professor Potonié to the group, and generally adopted.

The remarkable progress made in the last four or five years leaves no doubt that most, if not all, the members of this intermediate group, which embraces the majority of the Fern-like plants of the Palaeozoic, bore seeds. They have thus proved to be much nearer Gymnosperms than appeared before, but on account of vegetative and other characters they retain an intermediate position, and are now associated under the name Pteridospermeae. This class may be provisionally defined as:

Plants resembling Ferns in habit and in many of their anatomical characters, bearing seeds of a Cycadean type; seeds and microsporangia borne on fronds only slightly modified as compared with the vegetative leaves.

The Pteridosperms were thus, as Van Tieghem has said, "Phanerogams without flowers."

We will begin our account of the Pteridosperms with the family Lyginodendreae and the genus *Lyginodendron*, the type species of which now has the distinction of being the most completely known of all fossil plants (see Fig. 1, Frontispiece).

I. Lyginodendron

The species, or rather, perhaps, group of species, with which we are concerned at present is that named by Williamson *Lyginodendron oldhamium*.[1] Although the plant was first described by Binney, in 1866, it is mainly to Williamson's work that our present, very thorough knowledge of its vegetative structure is for the most part due. Fortunately, specimens of *Lyginodendron oldhamium* are among the very commonest remains contained in the calcareous nodules of the English Coal-measures; their preservation is often wonderfully perfect, so the material for investigation is altogether favourable.

The vegetative anatomy will be first considered, thus following the historical order in the progress of our knowledge, and subsequently the recently discovered seeds and male organs will be dealt with.

Both foliage and roots are now well known, and we are able to form a fairly accurate idea of the habit of the plant (see Fig. 1, Frontispiece). We will begin our description with the stem, the part to which the name *Lyginodendron oldhamium* was first applied,

[1] For nomenclature see Williamson, "Organisation of the Fossil Plants of the Coal-measures," Part iv., *Phil. Trans.* 1873, p. 377; also Williamson and Scott, "Further Observations, etc.," Part iii., *Phil. Trans.* 1895, B, p. 705. Potonié has re-named the genus *Lyginopteris*. See his *Lehrbuch der Pflanzen-palæontologie*, Leipzig, 1898, p. 160.

before its connection with the other organs was established.

1. *The Stem.*—The stems vary in diameter from about 3 mm. up to about 4 cm. The description will be based on the larger specimens, from 1 cm. in diameter upwards, as the smaller stems are in some ways exceptional, and will be best dealt with later.

The stem is, in all cases, of monostelic structure; the middle of the stele is occupied by a large pith, chiefly parenchymatous, but containing irregular groups of dark sclerotic tissue (see Figs. 129 and 130).

Around the pith are disposed several distinct strands of wood, varying in number from five to about eight or nine, and constituting the primary xylem of so many collateral vascular bundles (Fig. 129, *x*) Immediately outside the ring of primary xylem-strands, we find, in all except the youngest stems, a broad zone of secondary wood, consisting of radial series of pitted tracheides, with parenchymatous medullary rays, both principal and secondary, between them (Figs. 129 and 130). This zone was manifestly the product of a cambium, and, in fact, the cambial cells themselves are, in some of the specimens, quite evidently preserved at the exterior of the secondary wood (see Fig. 134, *cb*). Beyond the cambium is a well-marked zone of phloëm, also divided up by the rays, and for the most part of secondary origin. Opposite each of the primary xylem-strands, however, a group of primary phloëm can be recognised in well-preserved specimens (see Figs. 129 and 134, *ph*). We see, then, that the vascular structure, in its broad features, is that typical of the stems of normal Gymno-

sperms or Dicotyledons—a ring of collateral bundles, forming secondary wood and bast by means of a cambium.

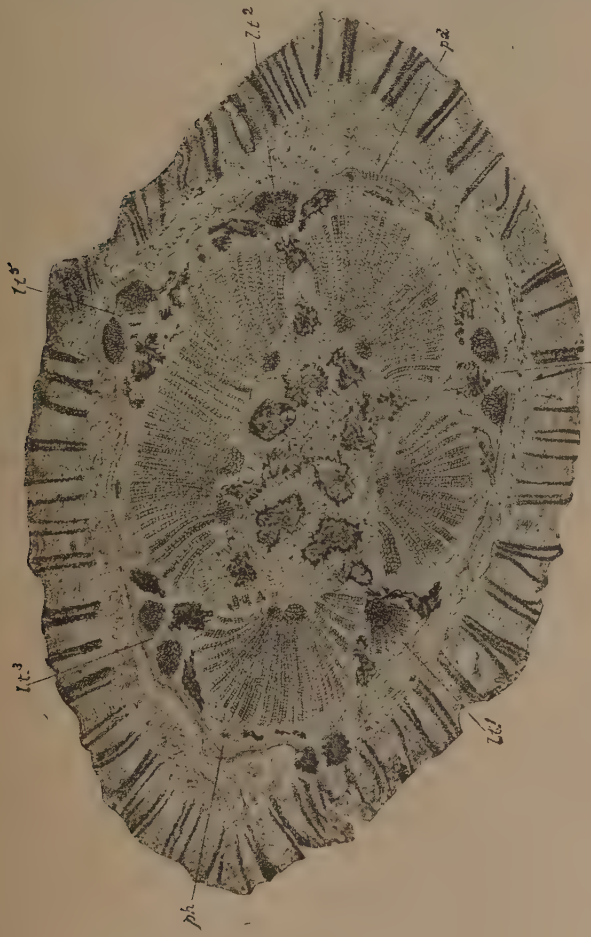

FIG. 129.—*Lyginodendron oldhamium*. Transverse section of stem. Surrounding the pith, which contains nests of sclerotic cells, are eight primary xylem-strands; beyond these is the wide zone of secondary wood, and then the phloëm. *ph*, a primary phloëm-group; *p.d*, periderm, marking the outer limit of the pericycle. Beyond the periderm is the inner cortex, and at the exterior, the outer cortex, with the dark radial bands of sclerenchyma. *l.t.*1—*l.t.*5, the five leaf-traces, numbered in the order of the phyllotaxis, *l.t.*5 belonging to the lowest leaf of the series. × 45. *Phil. Trans.*, W. and S. S. Coll. 270.

Beyond the phloëm-zone is a pericycle, containing groups of thick-walled elements, like those which occur in the pith. Embedded in the pericycle we find the

outgoing leaf-trace bundles, which are collateral in structure (Figs. 129 and 132). They keep a nearly vertical course for some distance, and do not leave the pericyclic zone until they bend out sharply through the cortex, to enter the bases of the leaves.

The outer cells of the pericycle have generally

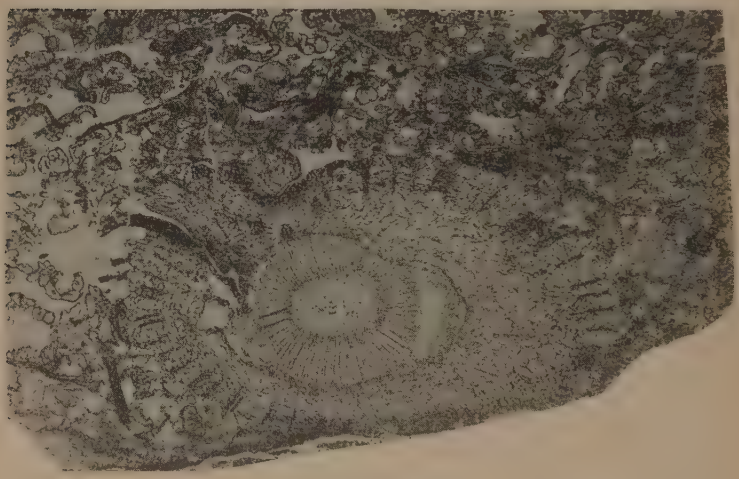

FIG. 130.—*Lyginodendron oldhamium.* Transverse section of stem (structure as in Fig. 129), surrounded by a mass of foliage, showing rachis and leaflets cut in various directions. On the left, the stem is giving off an adventitious root. × 4. From a photograph by Mr. L. A. Boodle. S. Coll. 636.

given rise to a few layers of periderm (Figs. 129, 132, 134, *pd*), which, however, does not reach any great development in *Lyginodendron*. Beyond the periderm we come to the thin-walled inner cortex, usually ill preserved, and then to the very characteristic outer cortex, consisting of interlacing strands of fibrous sclerenchyma, forming a network, with the meshes occupied by cellular tissue. In transverse section the

sclerenchyma appears in the form of dark radial bands (see Figs. 129 and 130). A few parenchymatous layers terminate the cortex towards the exterior.

The course of the vascular bundles through the stem is an important feature. The xylem-strands surrounding the pith constitute the downward continuation of the same leaf-trace bundles, which we find passing gradually outwards through the pericycle. That this is so is proved by our frequently meeting with the bundles in an intermediate position, on their way through the zone of secondary wood, which intervenes between pith and pericycle (Fig. 129, *l.t.*^{1}). When the leaf-trace is once clear of the secondary wood, it rises very steeply through the pericycle, following, as already mentioned, a nearly vertical course, but still passing slowly outwards, so that the pericycle is eventually bulged out to make room for it (see Fig. 129, *l.t.*^{5}). The trace, which on starting is a single bundle, divides into two, during its passage through the pericycle. The twin-bundles thus formed are very characteristic of the plant (see Figs. 129, *l.t.*^{3}-*l.t.*^{5}, and 132). The double trace finally bends out sharply through the cortex, and enters the base of a leaf-stalk (see Fig. ~~136).~~ ?138.

It is a very constant rule that, in any transverse section of the stem, five leaf-traces are present outside the wood. They are not all equally far out, and in good sections it is easy to tell which of them is nearest its exit into a petiole, and which is only just leaving the wood, and, in fact, to determine the exact order of all five (see Fig. 129). If we begin with the trace farthest inwards (*l.t.*^{1} in Fig. 129), we find that the

next outer one (*l.t.*^{2}) is separated from the former by $\frac{2}{5}$ of the circumference, the next outer one again (*l.t.*^{3}) by another $\frac{2}{5}$, and so on through the whole circuit. This arrangement of the leaf-traces points clearly to a $\frac{2}{5}$ arrangement of the leaves themselves, which is confirmed by direct evidence, when we have pieces of the stem long enough to show the bases of two or more leaves. The phyllotaxis, then, was a spiral one, with a divergence of $\frac{2}{5}$, at least in the larger stems. Of course phyllotaxis is a variable character ; in the very small stems of *Lyginodendron* there appears to have been a $\frac{1}{3}$ arrangement, and other divergences may very probably be met with.

As the leaf-traces of five successive leaves appear in the same transverse section, it follows that each leaf-trace must have extended through a length equal to five internodes, between leaving the wood and entering the petiole. As the internodes were often about an inch long, it is evident that the outward passage of the bundles was a very gradual one. The strands of wood around the pith are, as we have seen, continuous with the leaf-traces, and, in fact, form the lower part of the same system. Their number is less constant than that of the more external leaf-traces ; sometimes it is five, sometimes more. Where there are five xylem-strands only around the pith, they are alternate with the five leaf-traces in the pericycle. Where there are more than five, the excess is due to the fact that some of them are double ; their alternation with the outer traces is still maintained (Fig. 129). Each of the bundles surrounding the pith is, in fact, a sympodium, composed of the united lower ends of successive adjacent leaf-

traces. Where one of the circum-medullary xylem-strands is double (Fig. 129), one half is about to pass out to constitute a leaf-trace, while the other will continue the sympodium in a vertical direction.

We thus see that the entire vascular system of the *Lyginodendron* stem is built up of leaf-traces, in a manner comparable to that of the Gymnosperms or Dicotyledons, and in some degree to that of *Osmunda* among the Ferns.

The more detailed structure of the vascular tissues must now be considered. The primary xylem of the leaf-trace, whether examined at the margin of the pith, or at some point on its outward course, shows a constant arrangement of its elements. The small spiral tracheae (protoxylem) are invariably placed in the interior of the xylem-strand, but nearer its outer than its inner edge (see Figs. 131, 132, *px*). Thus the greater part of the primary wood in each bundle was developed centripetally, on the inner side of the protoxylem, while a smaller portion was formed centrifugally, on its outer side. The tracheides adjacent to the spiral primitive elements are scalariform, but the bulk of the primary wood, especially its centripetal portion, is formed of tracheides with bordered pits (cf. Fig. 157, p. 406, from *Heterangium*). A few parenchymatous cells adjoin the protoxylem (see Figs. 131 and 132), usually on the inner side. The bundles, as we have already seen, are collateral; this fact is most clearly seen in the outgoing leaf-traces (see Fig. 132), for in the bundles of the circum-medullary ring, xylem and phloëm are usually widely separated by the intercalated zone of secondary wood. Vascular bundles with the primitive elements

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in the interior of the primary wood are conveniently termed *mesarch*; those in the stem of *Lyginodendron* may thus be described as mesarch collateral bundles. This is a rare structure in recent plants, and, in fact, is almost limited to the leaves and petioles of Cycadaceae. The agreement between these foliar bundles and those in the stem of *Lyginodendron* is wonderfully close, as is

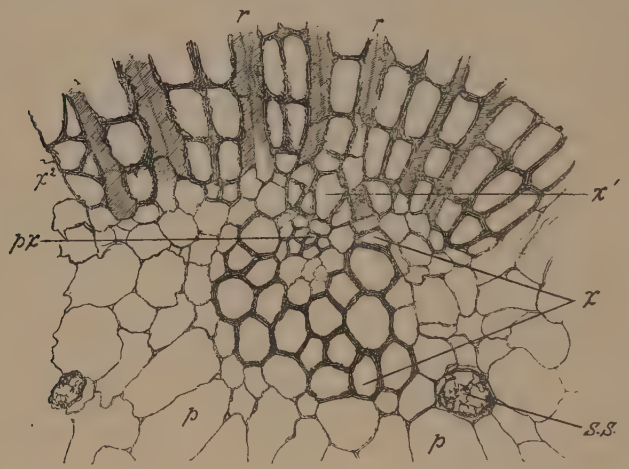

FIG. 131.—*Lyginodendron oldhamium*. Part of transverse section of stem, showing a primary xylem-strand, and adjacent tissues. *px*, protoxylem; *x*, centripetal primary wood; x^1, centrifugal primary wood; x^2, secondary wood; *r*, medullary rays; *p*, pith; *s.s.*, secretory sac. × 100. *Phil. Trans.*, W. and S. Will. Coll. 1884.

shown, for example, by the comparison of Fig. 132, representing a leaf-trace of *Lyginodendron*, with Fig. 133, drawn from a petiole of the recent *Stangeria*. In the *stem* of recent Cycads, however, the bundles are normal (endarch), with the spiral elements on the inner side of the wood. The occurrence of mesarch bundles in the stem of *Lyginodendron* and some other fossil plants, suggested a search for possible traces of the

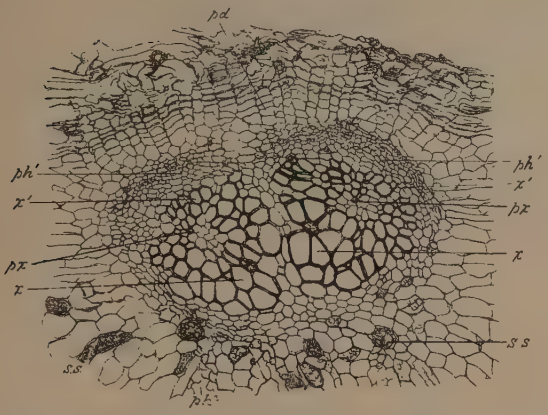

FIG. 132.—*Lyginodendron oldhamium.* Part of transverse section of stem, showing a double leaf-trace, and adjacent tissues. *px*, protoxylem of bundles; *x*, centripetal, x^1, centrifugal, part of xylem; ph^1, phloëm of leaf-trace; ph^2, phloëm of stele; *s.s.*, secretory sacs; *pd*, periderm. × about 40. *Phil. Trans.*, W. and S. Will. Coll. 1884.

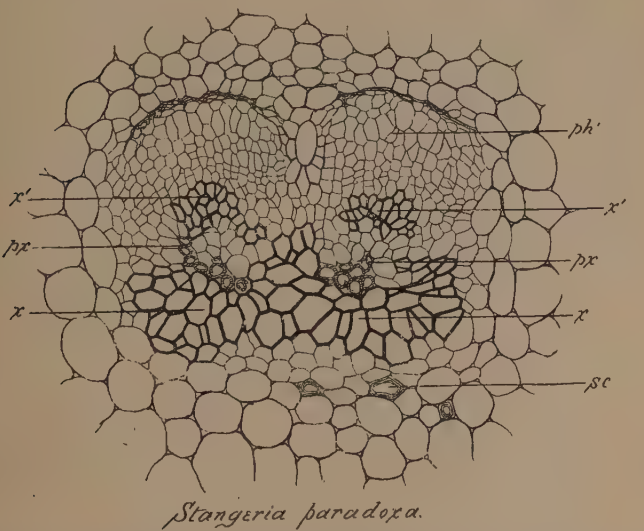

FIG. 133.—*Stangeria paradoxa.* Part of transverse section of petiole, showing a double bundle, to compare with Fig. 132. *sc*, stone-cell. Other lettering as in Fig. 132. × 95. From a drawing by Mr. G. Brebner.

same structure in the stems of recent Cycads, and the search was successful, for though no mesarch bundles have as yet been found in the vegetative stems, yet they occur distinctly in the peduncles of the cones in several Cycads, of the genera *Stangeria*, *Bowenia*, *Zamia*, *Ceratozamia*, and *Dioon*. In *Stangeria* and *Dioon* especially, the centripetal part of the xylem in these organs is still well developed, though in the others it is more reduced.[1] In these cases, then, the floral axis appears to have retained primitive characters, as is also shown in the simple course of its vascular bundles.

The secondary wood of *Lyginodendron oldhamium* forms a continuous ring, except where it is interrupted by the outward passage of a leaf-trace (Fig. 129). The fascicular and interfascicular cambium must have sprung into activity almost simultaneously (Fig. 135). The medullary rays vary much, both in height and width; they are sufficiently developed to have given the wood a somewhat soft parenchymatous character, approaching that of recent Cycadaceous woods. The tracheides are pitted on their radial walls only; the pits are multiseriate and bordered (cf. Fig. 157, p. 406, from *Heterangium*). Beyond the cambium (Fig. 134, *cb*), we come to the secondary phloëm (*ph*^{2}). Here the medullary rays become more or less dilated, breaking up the phloëm proper into narrow strands, each of which is made up of alternate tangential bands of large and small elements; the former were probably the sieve-tubes (Fig. 134). Where a leaf-trace bundle

[1] Scott, "The Anatomical Characters presented by the Peduncle of Cycadaceae," *Annals of Botany*, vol. xi. 1897, p. 399. F. W. South and R. H. Compton, "The Anatomy of *Dioon edule*," *New Phytologist*, vol. vii. 1908, p. 222.

passes out, a gap, filled by parenchyma, is left in the wood, which only closes up behind the bundle at a higher level (Fig. 129). When the leaf-trace leaves the wood of the stele, it is at first accompanied by its own secondary tissues, which, as seen in transverse section, form a fan-shaped mass on the outer side of the primary wood (see Fig. 129, *l.t.*[1]). As the strand

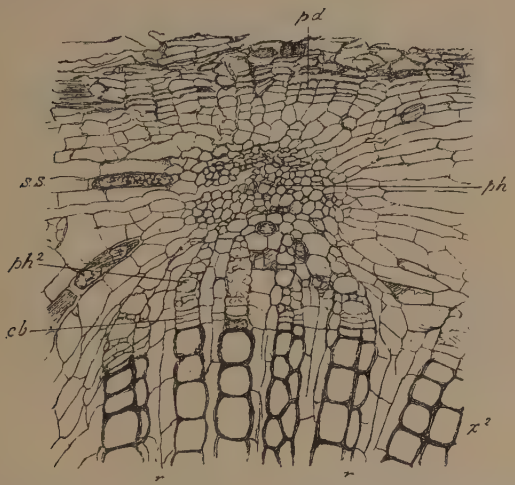

FIG. 134.—*Lyginodendron oldhamium.* Part of transverse section, from outer part of stele. x^2, secondary wood ; *r*, medullary rays ; *cb*, cambium ; ph^2, secondary, *ph*, primary, phloëm ; *s.s.*, secretory sac ; *pd*, periderm. × 52. *Phil. Trans.*, W. and S. Will. Coll. 1640.

passes up through the pericycle, this secondary portion is gradually lost, and has usually disappeared at the level where the bundle divides into two (see Figs. 129 and 132). The collateral structure, however, is still maintained. It is only where the leaf-trace finally bends out, to enter the petiole, that this structure changes. Here the phloëm begins to encroach on the inner side of the xylem, until, in the leaf-stalk itself, the

arrangement becomes completely concentric (cf. Fig. 138). Thus *Lyginodendron*, like *Osmunda* among recent Ferns, had collateral bundles in the stem, which became concentric in the leaf.

As regards the other tissues of the stem, little more need be said. Nests of thick-walled cells are abundant in the pith and pericycle, and extend out through the cortex into the petiole (Fig. 137). Sacs with dark contents, probably representing some kind of secretory organs, are frequent in all the soft tissues of the plant (Figs. 131, 132, 134). When considerable secondary growth had taken place, the cells of the more external tissues have often become much dilated tangentially, and this dilatation is naturally most conspicuous in the outermost tissues, namely in the parenchyma between the fibrous strands of the external cortex (Figs. 129 and 130).

Very curious, flask-shaped, multicellular outgrowths (Fig. 137, *e*) are often found on the surface of the stem, each consisting of an outer sheath of thick-walled cells, surrounding a parenchymatous core; the two tissues are continuous with the sclerenchyma and parenchyma respectively of the outer cortex. Very similar blunt spines occur on the petioles of some recent Tree-ferns, such as species of *Alsophila*. These emergences have been of great service in the investigation of *Lyginodendron*, for, as they occur on the leaves (Fig. 139, *e*) as well as on the stem, they rendered it possible to identify these organs as belonging to the same plant, before they had been found in actual continuity.

Very young twigs, still in the bud condition, which are sometimes met with, either detached or in connection with mature stems, are densely covered with the

spinous outgrowths, just as the young parts of recent Ferns are covered with the ramenta.

In addition to the spines, glandular outgrowths, apparently homologous with them, also occur, and in some forms of the plant are extremely abundant on stem, rachis, and leaflets. These organs, as we shall

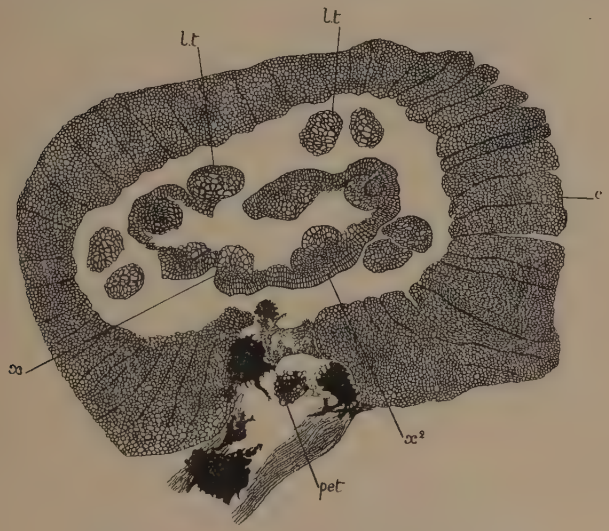

FIG. 135.—*Lyginodendron oldhamium*. Transverse section of a very young stem, at the commencement of secondary growth, *x*, one of the six primary xylem-strands surrounding the pith, which is not preserved; x^2, narrow zone of secondary wood; *l.t.*, leaf-trace bundles; *c*, outer cortex; *pet*, base of petiole. × 11. Will. Coll. 1144 D. (G. T. G.)

see, have played an even more important part than the spines in the advancement of our knowledge of the plant, for it was by means of the glands that the seeds of *Lyginodendron* were first identified (see p. 388). The glands are sometimes sessile, but more usually rested on a stout multicellular stalk, the actual gland consisting of a more or less spherical head, which is

filled by a small-celled secretory tissue (Fig. 136). In certain conditions the glandular tissue has broken down and the head is left empty (Fig. 146).

FIG. 136. — *Lyginodendron oldhamium*. Vegetative gland, showing well-preserved secretory tissue filling the head. The depression on the right of the stalk is a stoma. × about 60. S. Coll. 447. From a photograph by Mr. L. A. Boodle, F.L.S. (*Phil. Trans.* Oliver and Scott.)

We have so far described the ordinary structure of the *Lyginodendron* stem, such as is common to the great majority of the specimens. Sometimes quite young stems are met with, with little or no secondary growth; one of these is represented, in transverse section, in Fig. 135, at a stage when the secondary wood (x^2) was still quite thin. Such specimens show very clearly the identity of the leaf-traces (*l.t.*) with the strands (x) surrounding the pith. At this stage, the outer cortex contains only narrow bands of parenchyma; evidently this tissue increased by dilatation as the stem enlarged in girth.

In some cases small stems are found which are not merely young, but really have a different structure from the usual kind. Some of these little stems have a very small pith, surrounded by a more or less continuous ring of primary xylem, instead of by separate bundles. These specimens may very likely be the stems of

seedlings or very young plants, which had not yet attained their normal structure. We know that the embryonic stem of an *Osmunda* has a continuous ring

FIG. 137.—*Lyginodendron oldhamium*. Transverse section of branching stem. At the top of the figure is the base of a petiole containing two bundles. The stele of the branch lies below that of the main stem. × about 4. S. Coll. 2077. From a photograph by Mr. Tams.

of xylem, while, in the later-formed parts of the axis, this is gradually replaced by a ring of distinct bundles.

For many years after the discovery of *Lyginodendron* only unbranched stems came under observation, and it was not till 1902 that the first cases of branching were discovered by Mr. James Lomax. Fig. 137 shows, in

a transverse section belonging to a series cut from one of the original specimens, a stem about to give off a branch, which is still in connection with the main axis. A peculiar feature of the branching is that two of the leaf-traces in the pericycle of the main stem pass out into the branch, one on each side, and supply its first two leaves; the third leaf of the branch receives a trace from its own stele, passing out between the two former.

In some specimens branching of the stem has been found to be often repeated at short intervals, and in these cases it is always axillary, though it is not certain that this condition was constant. It is quite possible that the occurrence and mode of branching may prove to characterise distinct species still included under the collective name *L. oldhamium*.[1]

Various individual anomalies in the anatomical structure have been observed; the most frequent and interesting consists in the formation of secondary wood and bast, with inverted orientation, in the pith, immediately within the normal ring of bundles. The anomaly, in fact, is the same as that occurring in certain species of *Tecoma* and *Iodes* among recent Dicotyledons. It is evident that the anomalous cambium, giving rise to these medullary formations, was sometimes, if not always, continuous, through the trace-gaps, with the normal cambial zone. Thus it occasionally happened that each segment of the wood became completely surrounded by a zone of cambium, and grew in thickness on its own account, so that such a stem

[1] The branching of *Lyginodendron* has recently been fully investigated by Miss Brenchley, whose results are not yet published.

assumed a pseudo-polystelic structure. These anomalies, though only found in some specimens of *Lyginodendron oldhamium*, are interesting, not merely as an example of the plasticity of structure which the formation of cambium gives to a plant, but because they reappear, apparently as constant features, in some allied fossil stems.

2. *The Leaves.*—We have now to consider the evidence as to the nature of the *leaves* of *Lyginodendron oldhamium*. Almost every specimen of the stem of that plant is surrounded by a mass of finely divided foliage, the stalks and leaflets of which are cut in every direction by the plane of section. A good example is shown in Fig. 130, from a photograph. The main petioles of the leaves associated with the *Lyginodendron* stems are of large size, reaching a centimetre in diameter; they are often found branching, and the successive branches diminish in size, the ultimate ramifications being quite slender. The smallest of these are sometimes found in connection with the leaflets, which are deeply lobed, with veins diverging from one another at an acute angle. The material with structure preserved can only be studied in sections, and is more or less fragmentary, so that it is impossible to reconstruct, from it alone, a complete picture of the form of the highly compound leaf. Enough, however, is shown to enable us to identify these petrified specimens with certain fronds preserved as impressions, in which the whole configuration is manifest, and there is now no doubt that the foliage in question is identical with that of *Sphenopteris Höninghausi*, a form described

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by Brongniart as long ago as 1829[1] (see restoration, in Frontispiece).

It was suspected by Williamson, from the time of

Fig. 138.—*Lyginodendron oldhamium.* Radial§ section of stem, passing through the base of a petiole. x^2, wood of stem, enclosing pith; *pc*, pericycle; *c*, outer cortex; *pet*, petiole; the vascular bundle extends from the petiole down into the pericycle of the stem; *e*, cortical spines. × 3⅓. Will. Coll. 1982. (G. T. G.)

his first observations on the petioles of these leaves,

[1] The identity of the *Lyginodendron* foliage with this species of *Sphenopteris* has recently been demonstrated in detail by Mr. Kidston in his paper on the microsporangia of Pteridospermeae, cited below.

that they might belong to *Lyginodendron oldhamium*, an opinion which has since been raised to a certainty, by the discovery, in many instances, of the stem and petiole in actual connection (see Fig. 138, which shows the stem and petiole in radial section through the node). Before this discovery, the petioles were named

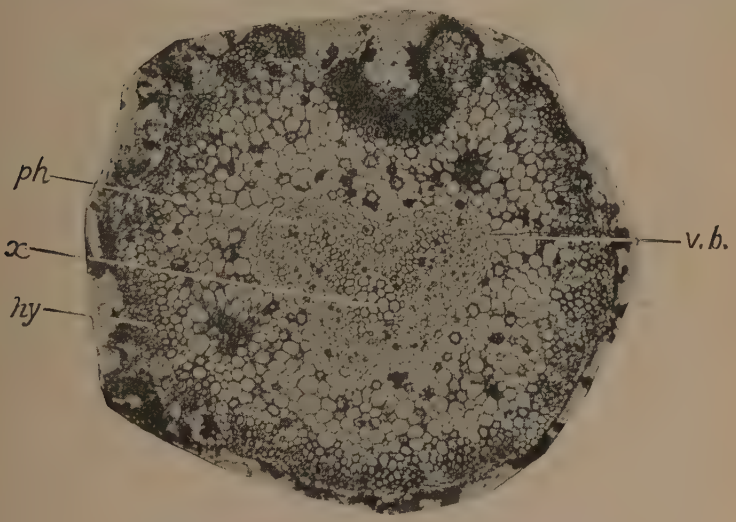

Fig. 139.—*Lyginodendron oldhamium*. Transverse section of rachis. *x*, V-shaped xylem; *ph*, phloëm, completely surrounding xylem, forming the concentric bundle *v.b.*; *hy*, hypoderma. × about 35. From a photograph. *Phil. Trans.*, W. and S. Will. Coll. 145.

Rachiopteris aspera. The petiole, which forked at some distance from the stem, to form two equal main branches of the rachis, contains either two distinct vascular bundles, or a single fused bundle, having the form in transverse section of a V or a W. In the finer branches of the rachis, the single V-shaped bundle is constant (see Fig. 139). The structure is in all cases concentric, the phloëm completely surrounding the

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xylem. In the specimen figured the preservation is surprisingly perfect, every cell of the phloëm being present. The convex side of the bundle is directed towards the lower surface of the petiole. The structure of the wood is like that of the primary bundles in the stem; the spiral elements occur in several groups in each bundle, and are placed in the interior of the xylem, towards its lower surface. In the specimen shown in Fig. 139 there are probably three protoxylem-groups, one near the bend of the V, and one towards the end of each arm.

The inner cortex contains bands of sclerotic tissue, like those in the stem, but more distinctly transverse, and the outer cortex is here also a network of fibrous strands, enclosing parenchyma in their meshes. The curious blunt spines, described above as occurring on the stem, are just as abundant on the leaf, where they are present on all parts of the petiole and rachis, and even extend onto the leaflets (see Fig. 140).

In some cases the minute structure of the leaflet is wonderfully well preserved (see Fig. 140); below the epidermis of the upper surface we can distinguish a hypodermal layer, beneath which again is well-characterised palisade-parenchyma. Towards the lower surface the mesophyll has a laxer structure, constituting the spongy parenchyma; occasionally, traces of stomata have been detected in the lower epidermis. The fine vascular bundles traversing the lamina are enclosed in distinct sheaths, and appear to have been collateral in structure, as is so often the case in the ultimate ramifications of the bundles in the leaves of recent Ferns. The whole structure is altogether comparable to that of a

fairly coriaceous Fern-leaflet at the present day, and indicates that the conditions to which the structure was adapted could not have been fundamentally different from those which prevail in our own epoch.

A xerophytic structure is clearly exhibited in the presence of a hypoderma, the considerable thickness of the leaflets, and their conchoid, incurved form. Such indications of xerophytic adaptation are exceedingly

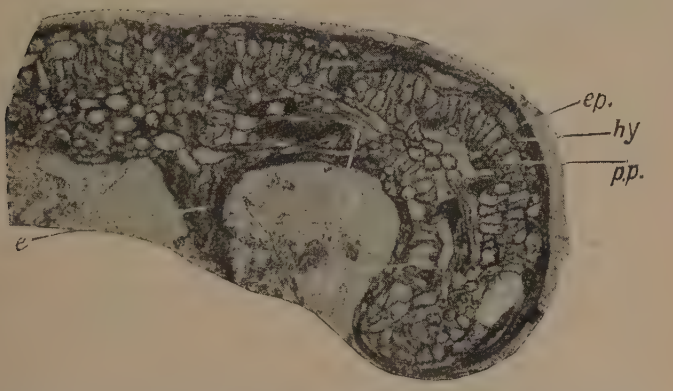

FIG. 140.—*Lyginodendron oldhamium*. Vertical section of a leaflet. *ep*, upper epidermis; *hy*, hypoderma; *p.p.*, palisade-parenchyma; *sp.*, spongy parenchyma; *v.b.*, vascular bundle; *e*, spine. × about 70. From a photograph. *Phil. Trans.*, W. and S. Will. Coll. 1196.

common among the plants of the Coal-measures, as already noticed in the case of *Sigillaria* (p. 225, vol. i.). The ends of the vascular bundles of the leaflets in *Lyginodendron* are commonly dilated as regards the xylem, a character which has also been observed in the xerophytic leaves of the Mangrove plants of tropical sea-shores.

The proof that the *Sphenopteris* form of foliage just described, which in structure, as well as in form and venation, is essentially Fern-foliage, really belonged to

Lyginodendron oldhamium, is clearly a point of great importance, for from the characters of the stem alone the affinity with Ferns is much less evident. This proof has been afforded, first, by finding the petioles in continuity, through their finer ramifications, with the *Sphenopteris* leaflets, and next, by finding the petioles themselves in continuity with the stem. The petiole is connected with the stem by a broad but not sheathing base (see Fig. 138). The twin leaf-trace bundles bend out sharply into the leaf-base, sometimes becoming fused as they enter it, sometimes remaining distinct. The sclerotic nests, already referred to, are very abundant in the cortex of the axillary region. The petioles found in connection with the stem can often be traced for some distance after they become free, and their branching can be followed; sometimes a fortunate section passes through the point of bifurcation of the main rachis. There is thus no doubt that the leaves of *Lyginodendron oldhamium* were of a forked and highly compound form. In all their characters, so far as the vegetative condition is concerned, they suggest the foliage of a Fern (see below, p. 384).

3. *The Roots.*—The adventitious *roots* of *Lyginodendron oldhamium* were known for many years as separate objects, before their relation to *Lyginodendron* was discovered. Like so many other detached organs of fossil plants, they received a distinct name, and were long known as *Kaloxylon Hookeri*. They have since been so constantly found in connection with the stem, that their true nature is fully established.

The roots are often most perfectly preserved, and

are beautiful objects, showing the characteristic points of root-structure with diagrammatic clearness. Some of the specimens are still in their primary condition, while others show the secondary tissues at all stages of their development. Some of the smallest rootlets are

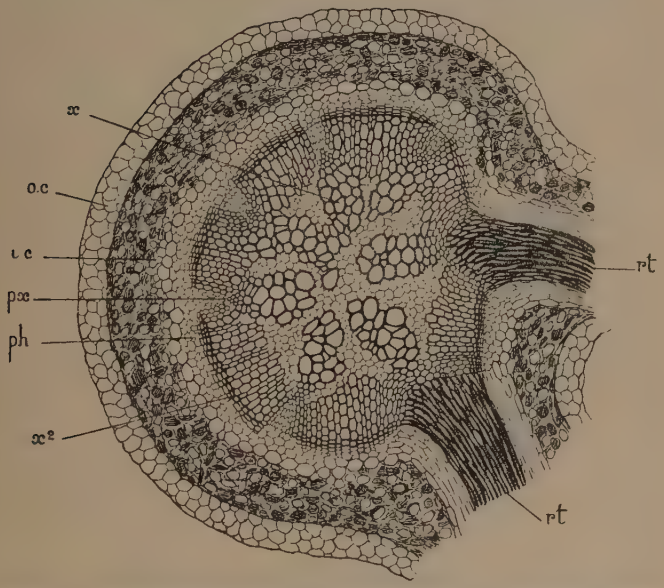

FIG. 141.—*Lyginodendron oldhamium.* Transverse section of root, somewhat diagrammatic. *px*, one of the protoxylem-groups; *x*, the heptarch primary wood; x^2 secondary wood; *ph*, phloëm; *i.c*, inner cortex; *o.c*, outer cortex; *rt*, rootlets, opposite two protoxylem-groups. × 24. Founded on S. Coll. 448. (G. T. G.)

triarch, or even perhaps diarch, but the larger and more characteristic specimens have from four to eight initial groups of xylem, alternating with as many strands of phloëm. The root shown in Fig. 141 was a heptarch one. The primary wood has a well-marked stellate form, as seen in transverse section (see Fig. 141). The smallest tracheides, which are shown by longitudinal

sections to be spirally thickened, are at the prominent angles (*px*), constituting a peripheral protoxylem, such as is characteristic of roots. Towards the interior the tracheides become rapidly wider, and assume pitted structure. They are intermixed with conjunctive parenchyma, which, however, never forms a definite pith. In good preparations the primary groups of phloëm, lying in the furrows of the wood, between the protoxylem-angles, can be clearly recognised, separated from the neighbouring wood by one or more layers of conjunctive parenchyma. The delicate, elongated elements of the phloëm are quite distinct, as seen in longitudinal section, from the adjoining parenchymatous cells. We thus see that there was a perfectly regular alternation of the xylem and phloëm-strands, just as in recent roots. A pericycle, one or more layers thick, surrounds the vascular tissue; the endodermis beyond this is often well defined, and in specially favourable cases its radial cell-walls stand out more sharply than the others. The broad inner cortex of the root consists of a lax parenchyma (Fig. 141, *i.c*), in which numerous elongated elements with dense carbonaceous contents, probably secretory sacs, are scattered. The outer border of the root is formed by a very well-defined double layer of large cells (*o.c*), generally well preserved, and constrasting sharply with the more perishable internal cortex. This double peripheral layer (exodermis) is one of the most useful characters in recognising the roots of *Lyginodendron*, though it was, perhaps, common to those of some closely allied genera. The roots, before secondary thickening set in, had a maximum diameter of about 5 mm.; they vary from this size

down to perhaps one-tenth of the diameter in the case of minute rootlets.

The roots branched freely ; their lateral appendages are always rootlets, *i.e.* the branches are decidedly smaller than the parent organ ; their branching was thus monopodial, as in Ferns or Cycads, not dichotomous, as in Lycopods. The rootlets were of endogenous origin, and their xylem is always in connection with one of the protoxylem-angles of the main root (see Fig. 141, *rt*). In these points, as in all others, the morphological character of these organs, as typical roots, is manifest.

Cases have recently been observed, by Professor F. E. Weiss and others, in which the structure of the root-apex is perfectly preserved. Details have not yet been published, but it appears that the growing point, unlike that of most Fern-roots, had no definite apical cell.

All the larger roots show, if old enough, well-marked secondary growth. Every stage of the process has been observed, showing that it took place exactly in the manner characteristic of the roots of Gymnosperms and Dicotyledons at the present day. The cambium first arose by the division of conjunctive cells, lying immediately within the phloëm-groups. The isolated cambial arcs thus formed were next united into a continuous zone, by the division of pericyclic cells lying outside the protoxylem-angles. Opposite each of these angles a principal ray was formed, and thus the secondary vascular tissue was at first broken up into distinct bundles, corresponding in number and position to the primary groups of phloëm (see Fig. 141, which shows the secondary tissues at a rather early stage of development). Subsequently, the principal rays became

partly filled up by the intercalation of intermediate strands of secondary wood and bast. The activity of the cambium was, in fact, in all respects normal; the secondary wood and bast agree in structure with the corresponding tissues in the stem. No distinct formation of periderm has been observed in these roots.

FIG. 142.—*Lyginodendron oldhamium*. Part of radial section of stem, showing an adventitious root, which is so curved as to be seen partly in longitudinal, partly in transverse section. x^2, secondary wood of stem; *pc*, pericycle; *o.c*, outer cortex; *a*, connection between root and wood of stem; *rt*, root, in transverse section, showing tetrarch structure, and giving off a rootlet. × 9. S. Coll. 466. (G. T. G.)

It is certainly a fact of great interest that the roots of our fossil, which, in their primary condition, much resemble those of recent Marattiaceous Ferns, or of *Helminthostachys* among the Ophioglossaceae, should exhibit a mode of secondary tissue-formation absolutely indistinguishable from that of typical Dicotyledons or Gymnosperms.

Naturally, all the roots of *Lyginodendron* with which

we are acquainted were adventitious. They are very commonly found in connection with the stem (see Fig. 142), where they are inserted indiscriminately on nodes or internodes, and on all sides alike. They are not, however, found on all portions of the stem, and were probably limited to its lower region (see restoration, in Frontispiece). By tracing characteristic specimens, with the structure of "*Kaloxylon Hookeri*," to their junction with the stem, proof was afforded that this fossil was simply the root of *Lyginodendron oldhamium*. The mode of connection between the adventitious roots and the stem affords proof that the former were endogenous organs, for the cortical tissues proper to the root can be traced throughout the whole thickness of the cortex of the parent stem. Fig. 142, from a radial section of the stem, shows clearly the connection of its tissues with those of the root. The latter happened to be bent, so as to show its transverse section, which is that of a tetrarch root with the structure of "*Kaloxylon*."

4. *Habit.*—We have already described the principal features in the structure of all the vegetative organs of *Lyginodendron oldhamium*. We may now attempt a reconstruction of the plant, so as to gain some idea of its habit, before going on to consider the subject of the organs of reproduction.

The stem must have been a comparatively slender one, of great length compared with its diameter. This appears to be proved by the length of the internodes (about an inch or so), and by the fact that every piece of stem shows, on the average, the traces of ten successive leaves (five traces outside the vascular ring,

and five or more around the pith). As the great majority of the specimens show no signs of any approach to the apex or base, it seems clear that they represent fragments of very long stems, bearing a large number of leaves. Although the stem was well constructed mechanically, thanks principally to the sclerenchymatous network of the outer cortex, it may be doubted whether an axis of such length and such slender proportions, bearing numerous leaves of large size, could have supported itself unaided in the vertical position. Yet the plant shows complete radial symmetry, and could not well have been of prostrate habit. It is not unlikely that *Lyginodendron oldhamium* was a climbing plant of the "scrambler" type, a suggestion which is confirmed by the presence of spines on the stem, and on all parts of the compound leaves. These spines may well have been organs of attachment, enabling the plant to cling to the trees or shrubs which supported it, just as we see in the recent Fern *Davallia aculeata*, where, however, it is only the frond, and not the stem that climbs. On the other hand, a comparison has been suggested with the tall, erect species of *Todea*, such as *T. australis*.

The evidence for the identification of the foliage of our fossil with *Sphenopteris Höninghausi* is now conclusive. The agreement is exact in the venation, form and size of the leaflets, and in their conchoid curvature, in the mode of branching of the rachis, the presence of spines on all the parts, and the reticulated cortex of the petiole. Further, casts have been figured by M. Zeiller, which agree closely with the stem of *Lyginodendron*, and which at the same time bear the

foliage of *Sphenopteris Höninghausi*.[1] The leaves of this species, which are very perfectly preserved as impressions, from the same horizon to which the specimens of *Lyginodendron oldhamium* belong, were of large size, and highly compound—tripinnate or more. There are various other species of Carboniferous Fern-fronds of very similar habit, and it is quite possible, as M. Zeiller[2] has suggested, that all may have belonged to stems of the *Lyginodendron* type.

The arrangement of the *Sphenopteris* leaves on the *Lyginodendron* stem, in $\frac{2}{5}$ phyllotaxis, has already been mentioned, and appears to agree with that of the specimens described by M. Zeiller. In the drawing[3] reproduced in the Frontispiece, an attempt has been made to give a restoration of the plant, as it would have appeared in nature. The slender stem (of which only the lower part could be included in the figure) is shown somewhat inclined, to indicate that it was probably supported by other plants. Its surface bears the characteristic spines, and shows traces of a reticulated cortical structure. The arrangement and form of the large, highly compound leaves are known, from the evidence given above, to be essentially true to nature, the lamina of the leaf having been copied from that of *Sphenopteris Höninghausi*. The forking of the main rachis, however, does not come out in the figure. The position of the branching adventitious roots on the

[1] Zeiller, *Bassin houiller de Valenciennes*, p. 84, Plate vi. Fig. 1, 1886. See also Kidston, "Microsporangia of Pteridospermeae," *Phil. Trans. R.S.* B, vol. 198, 1906.

[2] Zeiller, "Obs. sur quelques fougères des depôts houillers d'Asie Mineure," *Bull. Soc. Bot. de France*, vol. xiv. p. 195, 1897.

[3] Prepared, according to my instructions, by Mr. J. Allen, a skilful botanical artist.

stem is correct; some of them were borne on aërial parts of the stem, as shown in the figure, while others were, no doubt, entirely buried in the soil. The drawing was made before the discovery of the branching of the stem, which we now know to have occurred freely in many specimens (p. 371).

The pendulous, tufted bodies shown, in Fig. 1 (Frontispiece), on parts of the foliage, are intended to represent the lobed cupules, discovered by Stur in another species, and now known to have enclosed the seeds.

5. *The Seed.*—Up to the year 1903 our knowledge of *Lyginodendron* was practically limited to the vegetative organs. Any previous observations bearing on the mode of reproduction were then of uncertain significance; some of them will be referred to below. The first definite evidence was obtained by Professor F. W. Oliver, F.R.S., when he identified the seed of *Lyginodendron* by means of the glands on its enveloping husk.[1] The seed in question was named by Williamson (in MS.) *Lagenostoma Lomaxi*; the genus was founded by him, but he left this species undescribed.

The seed is barrel-shaped, and of rather small size compared with many other Palæozoic seeds, the extreme dimensions reaching 5.5 mm. in length by 4.25 mm. in maximum diameter. It is enclosed in an outer husk or cupule, which completely enveloped the seed when young (Fig. 143), though it was no doubt open at maturity (see Fig. 144, from a model). In one or two fortunate

[1] Oliver and Scott, "On *Lagenostoma Lomaxi*, the Seed of *Lyginodendron*," *Proc. Roy. Soc.* vol. lxxi. 1903; "On the Structure of the Palæozoic Seed *Lagenostoma Lomaxi*," *Phil. Trans. Roy. Soc.* (B), vol. 197, 1904.

FIG. 143.—*Lagenostoma Lomaxi.* Longitudinal section of a small seed, invested by the lobed cupule, which bears numerous glands. Micropyle and pollen-chamber well shown; chalazal tissue displaced. From a photograph by Mr. Boodle. Oliver and Scott, *Phil. Trans.* × about 15. Will. Coll. 1931, A.

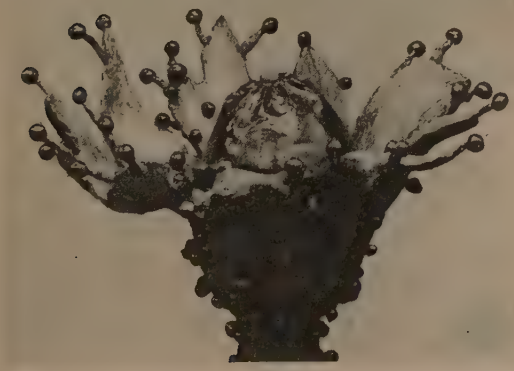

FIG. 144.—Restoration of the seed of *Lyginodendron* (*Lagenostoma Lomaxi*), from a model by Mr. H. E. Smedley. The seed is shown surrounded by the open glandular cupule.

cases the seed is found still attached to its pedicel; both pedicel and cupule are studded with capitate glands (Figs. 143, 144), usually borne on a stout, multicellular stalk. The cavity of the head is empty, and the whole structure is identical with that of the glands on the leaf

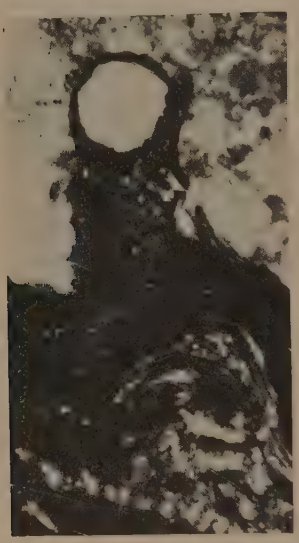

FIG. 145.—Capitate gland on the cupule of *Lagenostoma Lomaxi*. × 70.1 Oliver and Scott, *Phil. Trans.* S. Coll. 558.

FIG. 146.—Capitate gland on the petiole of *Lyginodendron oldhamium*. × 70. Oliver and Scott, *Phil. Trans.* Univ. College Coll. M 11, *e*.

Figs. 145 and 146 from photographs by Mr. Boodle.

and stem of *Lyginodendron*, at a stage when the secretory tissue has perished (compare Fig. 145, from the cupule of *Lagenostoma Lomaxi*, with Fig. 146, from a petiole of *Lyginodendron*). No other fossil plant is known with glands of this kind, and, considering the close and constant association of the seed with the vegetative organs of *Lyginodendron*, there can be no doubt as to

the correctness of the attribution. Further structural evidence is not wanting, as we shall see below.

The cupule, which in general form has been compared to the husk of a hazel nut, was ribbed in its lower part and divided into lobes above (see Figs. 144 and 149); it sprang from the pedicel immediately below the base of the seed, around which it formed a

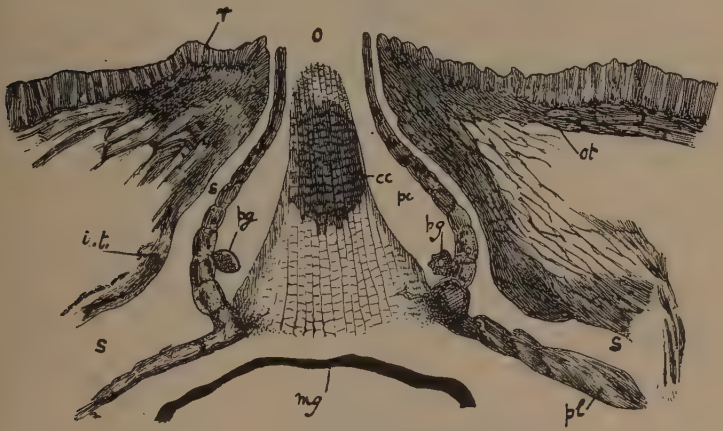

FIG. 147.—*Lagenostoma Lomaxi.* Apex of seed in median longitudinal section through micropyle. *r*, palisade-layer; *ot*, outer; *i.t.*, inner wall of canopy (integument); *s*, space between canopy and nucellus; *pc*, cavity of pollen-chamber; *o*, its orifice; *cc*, central column of pollen-chamber; *pg*, pollen-grains; *pl*, part of nucellus supporting pollen-chamber; *mg*, membrane of megaspore. × about 50. After Oliver. Univ. College Coll. R 1.

perfectly free envelope (see diagram, Fig. 148). The pedicel was traversed by a single concentric and mesarch vascular strand, which, before entering the chalaza of the seed, gave off a number of bundles (probably nine or ten) into the cupule; the cupular bundles were branched, and appear to have been collateral and mesarch in structure. There is a detailed agreement between the strands of the pedicel and cupule and those of the

rachis and leaflet, respectively, in the vegetative foliage of *Lyginodendron*. Thus all the evidence goes to show that the pedicel and cupule were of a foliar nature.

The seed itself is orthotropous, and, broadly speaking, of a Cycadean type; it shows perfect radial symmetry

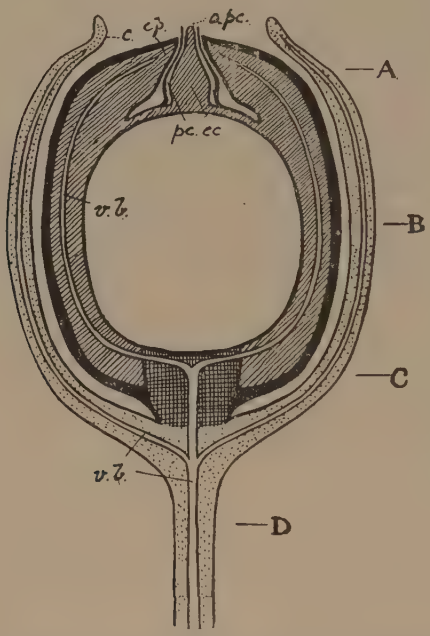

FIG. 148.—*Lagenostoma Lomaxi*. Diagram of seed in median longitudinal section. *c*, cupule; *v.b.*, vascular bundles of pedicel, cupule, and integument; *cp*, canopy of integument; *pc*, cavity of pollen-chamber; *cc*, central column; *apc*, orifice. A, B, C, D, planes of the transverse sections in Fig. 149. After Oliver.

(Fig. 149); the integument, which has a somewhat complex structure, is single, and completely adherent to the nucellus, except in the apical region (Fig. 148).

The central strand of the pedicel, after giving off the cupular bundles, passes straight up, and becomes the chalazal strand of the seed; it is here surrounded by a

mass of thick-walled strengthening tissue. The chalazal bundle then breaks up into the peripheral strands (usually nine in number) which traverse the whole length of the integument (Figs. 148 and 149). The

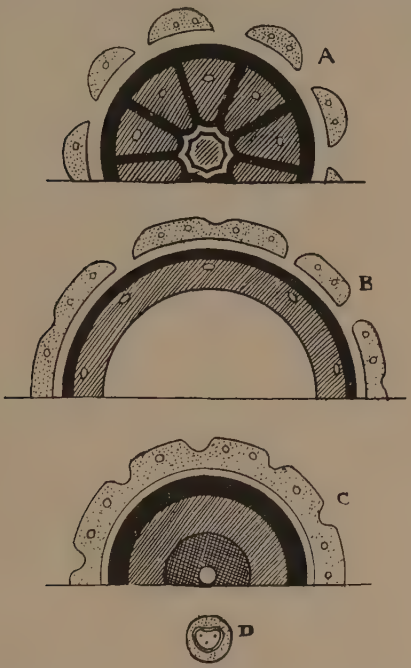

FIG. 149.—*Lagenostoma Lomaxi.* Diagrammatic transverse sections in the planes A, B, C, and D of Fig. 148. A (through micropyle) shows pollen-chamber canopy of integument and free lobes of cupule; B (through body of seed) shows fused nucellus and integument, with vascular bundles, and cupule partly divided into lobes; C (through chalaza) shows central bundle, chalazal tissue, base of integument, and continuous, furrowed cupule; D, section of the rachis-like pedicel. After Oliver.

latter expands in its free part, towards the micropyle, into the chambered "canopy," a ring of nine loculi, separated from each other by thick partitions, but filled by a delicate tissue which has commonly perished. Into each of these loculi, one of the nine vascular bundles

entered, and there terminated (see Fig. 149, A). The canopy may represent a provision for water-storage, serving, perhaps, as has been suggested, to supply the necessary liquid for pollination by means of a "drop-mechanism." The outer layer of the integument has a columnar or palisade-like structure; there is some evidence that a secretion of mucilage took place from this layer, as in the testa of so many recent seeds.

As in the recent Cycads and in *Ginkgo*, the free apex of the nucellus forms the pollen-chamber, a cavity for the reception of the pollen-grains,[1] which in the case of *Lagenostoma* has a peculiar and characteristic form, for a solid column of tissue rises up in the middle of the chamber, leaving only a narrow annular space, in which the pollen-grains are found (Figs. 143, 147, 148, 149, A). The outer wall of the flask-shaped pollen-chamber projects a little through the micropyle, as an open tube, and no doubt received the pollen-grains directly, without their having first to traverse a micropylar passage (Figs. 147 and 148). The pollen-grains occurring in the chamber appear to have been multicellular, but this point is better shown in other cases (see Figs. 173 and 174, pp. 458 and 459).

The interior of the seed has not been found in a good state of preservation. The outlines of the mega-spore or embryo-sac can usually be traced, but its membrane cannot always be distinguished from the disorganised tapetal layer of the nucellus.

The discovery of the seed of *Lyginodendron* afforded, for the first time, the proof that a member of the Cycadofilices was a seed-bearing plant, and led, as

[1] For the pollen-chambers see Chap. XII. p. 542.

further evidence came in, to the establishment of the new class Pteridospermeae.

The seed is, as we have seen, a complex one, and already far removed from the Cryptogamic megasporangium ; there is indeed little trace of anything primitive in *Lagenostoma* beyond the fact that the reception of the pollen was still left to the nucellus—the sporangial part of the seed—and not yet assumed by the integument. The absence of any trace of an embryo is a negative character common to all known Palæozoic seeds, though there are many instances of the preservation of archegonia (see, for example, Fig. 198, p. 549). Yet the seeds, as a rule, are evidently mature and not mere ovules. Neither, considering the frequent presence of pollen-grains in the pollen-chamber, can we assume that all the seeds found happened to be barren. It is possible that, though pollinated, they were not yet fertilised, the latter process taking place an appreciable time after the seed was shed ; or again, it may be that a resting stage followed immediately on fertilisation before any marked development of the embryo had taken place. In any case it appears that in these ancient seeds the period of rest came much earlier with reference to the growth of the embryo than in most of our recent seeds.[1] We find a relic of the old conditions in living Cycads, in which the embryo is often scarcely to be recognised when the seed is ripe and ready for sowing.

Returning to the seed of *Lyginodendron*, we have seen that the structure of the pedicel shows that the

[1] It is interesting to see that the Mesozoic *Bennettites* was completely modern in this respect, for there the embryo was far advanced, and filled the whole embryo-sac before the seed was shed (see Fig. 205, p. 574).

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seed-bearing organ formed part of a leaf. Evidence from closely allied species leaves no doubt that the seeds were borne on compound fronds or pinnae, only differing from the sterile foliage in the suppression of the laminae of the leaflets, or rather, perhaps, their modification to form the cupules.

Calymmatotheca Stangeri, a fructification of Lower Carboniferous age, discovered by Stur in 1877,[1] consists of stellate, usually six-rayed bodies, borne on a naked branched rachis. A reinvestigation of the specimens has confirmed Stur's attribution of the fructification to a *Sphenopteris* closely similar to *S. Höninghausi* (the foliage of *Lyginodendron oldhamium*), and also his interpretation of the stellate bodies as foliaceous indusia, and not groups of sporangia. There is little doubt that these organs[2] are of the same nature as the cupules of our *Lyginodendron*, but in Stur's specimens the seeds had been shed, perhaps prematurely.

FIG. 150.—*Lagenostoma Sinclairi*. Portion of branched rachis, bearing cupulate seeds. Nat. size. After Arber.

Mr. Arber has described a seed, *Lagenostoma Sinclairi*, Kidston, of Lower Coal-measure age, which agrees closely in external characters with *L. Lomaxi*, and, like the latter, is invested in a lobed cupule (Figs. 150 and 151). The cupulate seeds were borne on the terminations of the finer branches of a highly compound frond, with reduced lamina, in all

[1] Stur, "Die Culmflora der Ostrauer u. Waldenburger Schichten," *Abhandl. d. k. k. geol. Reichsanstalt zu Wien*, vol. viii. Part ii.

[2] Indicated in the restoration of *Lyginodendron* in Fig. 1, Frontispiece.

probability of the *Sphenopteris* type.[1] The character of the seed itself suggests the presence of a "canopy."

In *Sphenopteris Dubuissonis*, a Lower Coal-measure species from Brittany allied to *S. Höninghausi*, M. Grand'Eury has observed six-lobed cupules, in some cases still containing the seeds, situated at the extremity of long, slender pedicels, identical with the ultimate ramifications of the rachis.[2]

FIG. 151.—*Lagenostoma Sinclairi*. Two seeds, enclosed in lobed cupules, and borne terminally on branches of the rachis. × 5. After Arber.

The specimens described by Stur, Arber, and Grand'Eury are all preserved in the form of impressions; they supplement, in a most satisfactory manner, the evidence of the structural specimens, and leave no doubt that the seeds of the *Lyginodendron* group were borne on the rachis of the frond. The analogy of the pollen-bearing organs, next to be described, establishes a presumption that the fertile rachis formed part of the same frond which elsewhere bore vegetative leaflets.

The well-known seed *Lagenostoma ovoides*, of which

[1] Arber, "Some New Species of *Lagenostoma*, a Type of Pteridospermous Seed," *Proc. Roy. Soc.* (B) vol. lxxvi. 1905.

[2] Grand'Eury, "Sur les Graines de *Sphenopteris*," etc., *Comptes Rendus* t. 141, p. 812, 1905.

the structure was described by Williamson, agrees so closely with *L. Lomaxi* that it must clearly have belonged to some plant of the *Lyginodendron* type. *Physostoma elegans*[1] (= *Lagenostoma physoides*), another of Williamson's discoveries, is more remarkable, and perhaps more primitive, for here the micropylar tube is replaced by a ring of about ten free tentacles, surrounding the apex of the nucellus, and apparently corresponding to the loculi of the canopy in *Lagenostoma*. In neither of the seeds last mentioned has a cupule as yet been discovered.

6. *The Microsporangia.*—Nothing certain was known of the male fructification of *Lyginodendron*, or indeed of that of any Pteridosperm, until Mr. Kidston, in 1905, discovered a species of *Crossotheca* (*C. Höninghausi*, Kidston) in organic connection with the foliage of *Lyginodendron*.[2] The genus *Crossotheca* was founded by Zeiller in 1883,[3] on a fructification found by him in connection with a *Sphenopteris* (see Fig. 109, F, Vol. I. p. 280); the genus was characterised by the arrangement of the sporangia, hanging from the lower surface of the oval or spathulate fertile segments, the whole resembling an epaulet with its fringe. On account of the absence of an annulus and the appearance of a slight fusion between the sporangia, Zeiller referred *Crossotheca* to

[1] A full investigation of this seed by Professor F. W. Oliver has appeared in the *Annals of Botany* for January 1909.

[2] Kidston, "On the Occurrence of Microsporangia in Organic Connection with the Foliage of *Lyginodendron*," *Proc. Roy. Soc.* (B) vol. lxxvi. p. 358, 1905; "On the Microsporangia of the Pteridospermeae," *Phil. Trans. Roy. Soc.* B, vol. 198, 1906.

[3] "Fructifications de Fougères du Terrain Houiller," *Ann. sci. nat. Bot.* sér. vi. t. xvi.

the Marattiaceae, a view which was generally adopted

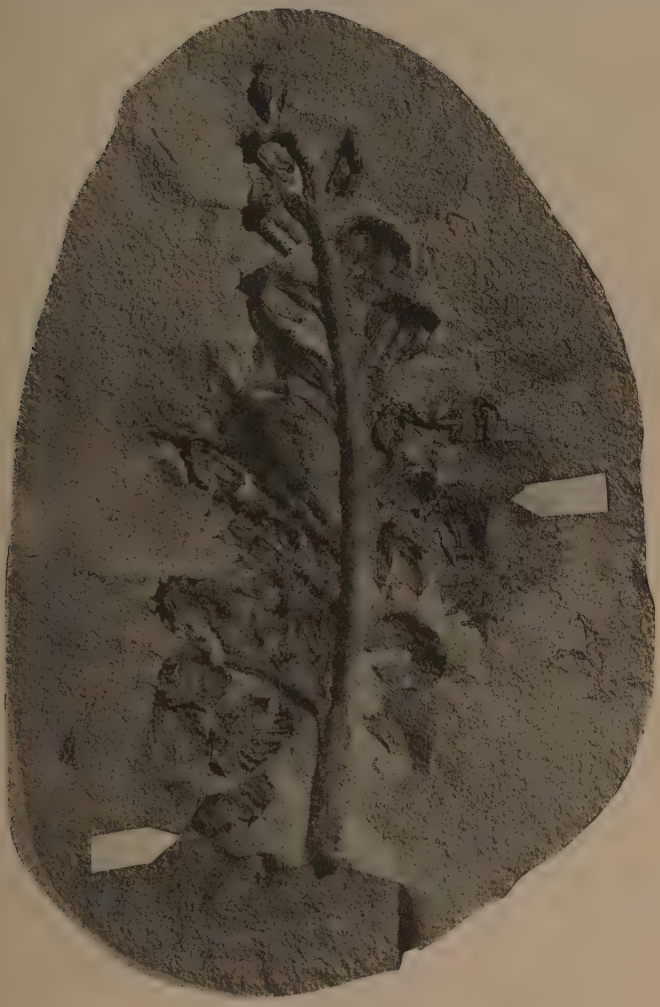

FIG. 152.—*Crossotheca Höninghausi* (the microsporangiate fructification of *Lyginodendron oldhamium*). Fertile pinna, contained in an ironstone nodule. On the ultimate branches of the rachis are borne the somewhat peltate fertile pinnules, from the under surface of which the long microsporangia hang down. × 3. Enlarged from a photograph lent by Mr. R. Kidston, F.R.S.

up to the date of Mr. Kidston's discovery. In the meantime a number of other species had been described, some with the Sphenopterid and others with the Pecopterid type of foliage.

Mr. Kidston's specimens were found in ironstone nodules from the Dudley Coal-field (Westphalian series) (Fig. 152). The specimens are preserved in the form of casts, but the cavities in some cases are infiltrated with carbonate of lime, and so retain their natural form, with some degree of structural preservation. Though most of the fertile specimens bear no sterile pinnules, in some cases the two forms occur in organic connection (see Fig. 153), proving that the *Crossotheca* was borne on foliage identical with that of *Lyginodendron*. Fig. 152, from a photograph, shows clearly the general structure and arrangement of the fertile pinnules, which are oval in form, about 2-2.5 mm. in length, and borne on stout pedicels, the mode of insertion rendering them somewhat peltate. The pinnule is of some thickness, and appears to be traversed by a branched vein. "Each fertile pinnule usually bore six, rarely seven, bilocular microsporangia. They are fusiform and end in a sharp point."[1] The sporangia are described as convergent

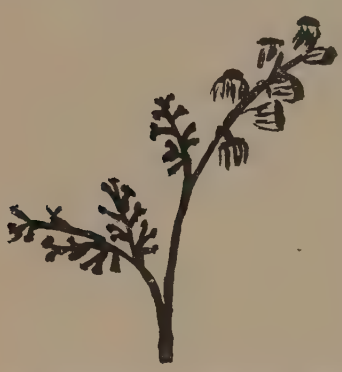

FIG. 153.—*Crossotheca Höninghausi*. Fertile pinna in connection with sterile pinnae of *Sphenopteris Höninghausi* (leaf of *Lyginodendron*). × 2. R. S. From a sketch after a photograph lent by Mr. Kidston.

[1] Kidston, *Microsporangia of Pteridospermeae*, p. 421.

when young, but opening out later, and then assuming the fringe-like arrangement. They are about 3 mm. long and 1.5 mm. in maximum width, while each loculus has a diameter of about .5 mm.

No evidence of cohesion among the sporangia was observed, but each "bilocular sporangium" may be interpreted as a synangium, though this does not appear to be Mr. Kidston's view. The nature of the preservation is such as to leave the detailed morphology somewhat uncertain. The microspores were still contained in the cavities of the sporangia, and could be studied in some detail. Each spore has a distinct triradiate ridge, indicating tetrahedral development, and the surface of the outer wall is rough with minute points. The diameter of the spore varies from .05 to .07 mm.

Mr. Kidston finds that "the cleft by which dehiscence took place passed longitudinally down the centre of the inner face of the microsporangium, and thus the microspores of both loculi would be liberated simultaneously."

Mr. Kidston observed in the Dudley nodules, another species of *Crossotheca*, *C. Hughesiana*, which has cordate fertile pinnules, but is otherwise closely similar to *C. Höninghausi*.

Shortly before Mr. Kidston's discovery of the connection between *Crossotheca* and *Lyginodendron*, Miss M. Benson, D.Sc., described a fructification (*Telangium Scotti*) with structure preserved, from the Coal-measure nodules, and was inclined to attribute it to *Lyginodendron*.[1]

[1] Benson, "*Telangium Scotti*," *Ann. of Bot.* vol. xviii. 1904. A preliminary note was published two years earlier.

The sporangia are long and pointed, resembling those of Mr. Kidston's *Crossotheca* in shape and size, but are united in their lower part to form large synangia often with as many as eight members.

Miss Benson described the synangia as borne terminally on the ultimate ramifications of a rachis, but I have since satisfied myself that they were in reality seated on a flat disc or lamina, quite comparable to a fertile pinnule of *Crossotheca*. Thus the most important of the distinctions enumerated by Mr. Kidston (*l.c.* p. 424) between *Crossotheca* and *Telangium Scotti* is removed, and I have little doubt that Miss Benson's fossil will find a place in the genus *Crossotheca*. The possible relation of *Telangium Scotti* to *Lyginodendron* requires further investigation, but it is not unlikely that it may prove to belong to one or other of the forms at present grouped under the name *Lyginodendron oldhamium*.[1]

It may be mentioned that in the same petrifactions in which *Telangium Scotti* occurs, bisporangiate synangia have lately been observed, but with the additional complication that each sporangium is subdivided into two loculi. It is possible that these specimens may have belonged to one of Mr. Kidston's species of *Crossotheca*.[2]

Though many interesting questions as to the male fructification of *Lyginodendron* still await solution, the main point is made clear by Mr. Kidston's discovery that *Crossotheca*, hitherto assumed to be the fertile frond

[1] An interesting point emphasised by Miss Benson is the resemblance of the spores of *Telangium* to the pollen-grains found in the pollen-chamber of *Lagenostoma ovoides*.

[2] I am indebted to my friend Professor F. W. Oliver, F.R.S., for my knowledge of these preparations.

of a Fern, constitutes the pollen-bearing organs of this genus of Pteridosperms, a fact that must affect our judgment on many other Palæozoic fructifications. In bearing its microsporangia on a pinna of the same frond which in other parts has purely vegetative characters, *Lyginodendron* shows a lower degree of differentiation than any Seed-plant previously known. The reproductive organs of this genus present the same combination of characters which we found in the vegetative structure. While the highly organised seed indicates a clear affinity with Cycadophyta, the microsporangiate organs are of a more Fern-like nature.

Lyginodendron oldhamium has been described at considerable length because, from our exceptionally complete knowledge of the plant in all its parts, it may best serve as the type of the Pteridospermeae. We now pass on to review, more briefly, other representatives of the class.

II. Heterangium

Several species of this genus have been described, some from our own country, others from the Carboniferous strata of France and Germany. The geological range of these plants is considerable, for some species have been found in the Calciferous Sandstone rocks of Scotland, at the very base of the Carboniferous formation, while others appear in the Coal-measures, and others again in the Permian beds of Autun, in France. Our description will be based, in the first instance, on the *Heterangium Grievii* of Williamson, the oldest of the species at present described, and the one which

happens also to have been most completely investigated. The specimens, with structure preserved, were first discovered in 1871, among the calcified remains brought to light in that year by Mr. G. Grieve, at Pettycur, near Burntisland, in Scotland; the horizon of this bed, which has often been referred to above, is that of the Calciferous Sandstones. The plant was described by Williamson, who at first named it *Dictyoxylon Grievii*, but shortly afterwards (1872) placed it in Corda's genus *Heterangium*, which up to that time had only been known from a single fragment.

In the case of *Heterangium* we have as yet no certain knowledge of the reproductive organs, and the reference of the genus to Lyginodendreae is therefore based entirely on vegetative characters.

The specimens of *Heterangium Grievii* are numerous in the Burntisland deposit, and the structure is often very well preserved, as in the specimen represented, in transverse section, in Fig. 155. To quote Williamson's words, it "always appears in the form of straight, slender, unbranched stems." Branching, however, may have occurred occasionally, for we have found one instance in a closely allied species (*H. Lomaxii*), but in any case it must have been rare. The restoration of a portion of stem, shown partly in section and partly in surface-view, reproduced in Fig. 154, from Williamson's original memoir,[1] gives an accurate idea of the general structure. In external form the stems, which have not been found to exceed about 1.5 cm. in diameter, are angular; the projecting ribs are

[1] "Organisation of Fossil Plants of Coal-measures," Part iv., *Phil. Trans.* 1873.

formed by the decurrent bases of the spirally arranged leaf-stalks (Fig. 154). The general character of the foliage is known; the leaves, like those of *Lyginodendron oldhamium*, were highly compound, and are referable to the *Sphenopteris* type (cf. Fig. 160). There is, in fact, good evidence for the identification of *Heterangium Grievii* with a definite species of *Sphenopteris*, but before entering into this question it will be necessary to describe the organisation of the specimens with structure preserved.

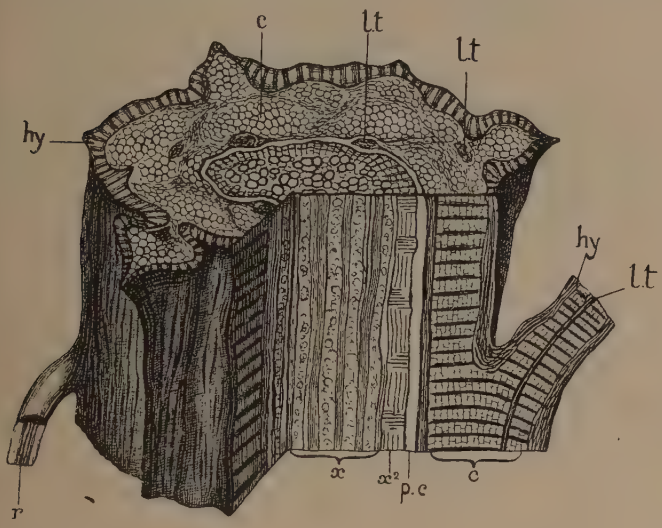

FIG. 154.—*Heterangium Grievii.* Restoration of a portion of the stem, showing transverse and longitudinal section, and part of the external surface. *x*, primary wood of stele; x^2, secondary wood; *pc*, phloëm and pericycle (left blank); *c*, cortex, with horizontal sclerotic bands; *hy*, hypoderma of stem and petiole; *l.t*, leaf-traces, one of which is entering the petiole; *r*, adventitious root. The bases of several petioles are shown. Enlarged. After Williamson, *Phil. Trans.*

1. *The Stem* (*H. Grievii*).—The stem of *Heterangium*, like that of *Lyginodendron*, had a single vascular

cylinder, from which the leaf-traces were given off. The stele differs, however, from that of the other genus in one striking point; in *Heterangium* the whole interior of the stele is occupied by the primary wood

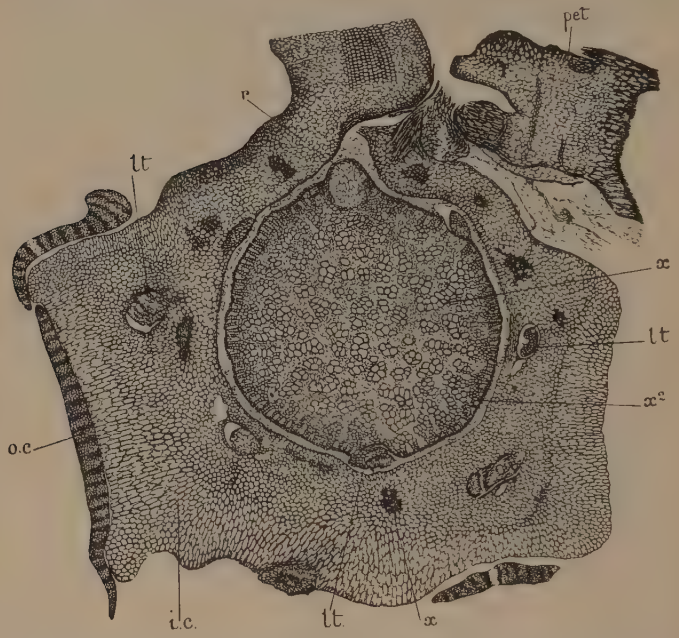

FIG. 155.—*Heterangium Grievii*. Transverse section of stem. *x*, central mass of primary wood, consisting of tracheides and parenchyma; x^2, secondary wood, beginning to form; next come phloëm and pericycle; *i.c*, inner cortex (*x* in this zone is a sclerotic group); *l.t*, leaf-traces; *r*, base of an adventitious root; *o.c*, outer cortex or hypoderma (only present in places); *pet*, base of petiole, partly detached. × about 5. S. Coll. 396. (G. T. G.)

(see Figs. 154 and 155), which extends to the centre, leaving no pith whatever, while in *Lyginodendron*, as we have seen, the large pith is a constant feature. The difference is so striking that it might seem, at first sight, to preclude the idea of any close relationship between the two genera; yet, as Williamson at once

recognised, and as all subsequent research has confirmed, the evidence of consanguinity is clear and convincing.

The primary wood in *Heterangium* is composed throughout of irregular anastomosing groups of tracheae, interspersed with strands of conjunctive parenchyma

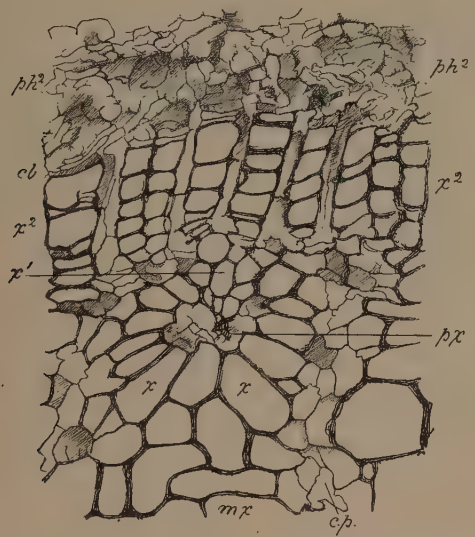

FIG. 156.—*Heterangium Grievii.* Part of transverse section, from outer part of stele, showing a primary xylem-strand and adjacent tissues. *px*, protoxylem of strand; *x*, centripetal, x^1, centrifugal, primary wood; *mx*, metaxylem, *c.p*, conjunctive parenchyma; x^2, secondary wood; *cb*, cambium; ph^2, phloëm. × 135. *Phil. Trans.*, W. and S. Will. Coll. 1293.

(Figs. 154 and 155, *x*). As a rule, the tracheae are more abundant than the parenchyma, and even where the reverse is the case, there is never any aggregation of the cellular tissue to form a pith. The structure of the primary wood is not, however, uniform in all its parts. Around its periphery, definite clusters of tracheides can be distinguished, each of which agrees

exactly in structure with one of the primary strands of xylem in *Lyginodendron* (compare Fig. 156 with Fig. 131). The smallest elements of the cluster are internal, lying at a short distance from its outer limit (Fig. 156, *px*); these smallest elements are shown by longitudinal sections to be tracheides, with a lax spiral thickening; they thus constitute the protoxylem of the bundle (Fig. 157, *px*). They are succeeded towards the exterior by more densely spiral or reticulate tracheides, of somewhat larger size (Figs. 156 and 157, x^1). The protoxylem is accompanied by a little parenchyma, and the rest of the primary strand, including all its lateral and interior part, is formed of large tracheides, with multiseriate bordered pits, as in *Lyginodendron* (Figs. 156 and 157, *x*). Similar pitted elements extend throughout the whole interior of the stele, forming the mass of primary wood. The central wood, as distinguished from the peripheral xylem-strands, may be termed the *metaxylem*. From the nature of the case, the primary strands are not obviously distinct, as in the former genus, but they are characterised at once by their mesarch structure, and by the fact that they alone

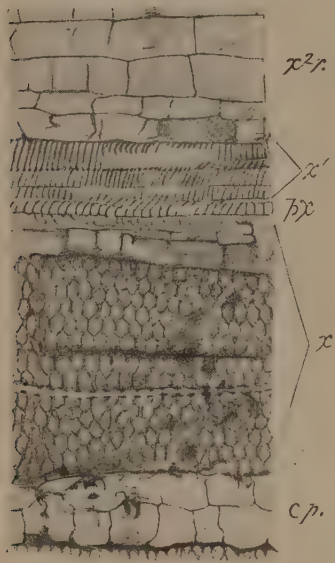

FIG. 157.—Corresponding longitudinal section, showing the structure of the tracheides. x^2r, parenchyma at the commencement of a medullary ray. Other lettering as in Fig. 156. × 135. *Phil. Trans.*, W. and S. Will. Coll. 1266.

are continued outwards into the cortex, to form the xylem of the foliar bundles. The stele of *Heterangium* thus differs from that of *Lyginodendron* in the fact that in the former the xylem extends through the whole central region, forming a continuous mass of primary wood, traversed by irregular bands of conjunctive parenchyma, but without a pith.

In some stems this primary structure has remained unaltered; in such cases, the phloem, which, no doubt, formed a zone round the wood, can only be recognised as a ring of imperfectly preserved tissue. Most specimens, however, had already produced secondary wood and phloem, though not usually to so great an extent as in *Lyginodendron*. The secondary wood consists of rather small tracheides, arranged in regular radial series, with medullary rays between them (see Figs. 154, 155, and 156, r^2). The secondary tracheides bear numerous bordered pits, which are usually limited to the radial walls. Beyond the wood the cambium and secondary phloem are often fairly well preserved (see Fig. 156, *cb*, ph^2). In all cases, whether secondary thickening had taken place or not, the stele is surrounded by a well-marked pericycle, consisting of several layers of thin-walled parenchyma.

The wide inner cortex has a very characteristic structure. Its ground-mass consists of short-celled parenchyma, but in this tissue numerous horizontal plates of thick-walled mechanical elements are embedded (see Fig. 154, *c*). The sclerotic plates do not extend all round the stem, but are isolated and ranged in vertical series. Thus, a radial section of the stem may either show a whole row of them, one above the other,

or, if it happen to pass between two series, may miss them altogether. The cells of which the sclerotic plates are composed are short, and similar in structure to the stone-cells of many recent plants. The transversely striated appearance, which these plates give to the cortex, often serves to identify *Heterangium* at once, even on a naked-eye inspection of rough specimens or carbonised impressions (cf. Figs. 159 and 160).

The outer cortex, or hypoderma, is formed of alternating strands of fibres and parenchyma (Figs. 154, *hy*, and 155, *o.c*). The structure, as seen in transverse section, is much like that of the same region in *Lyginodendron*, except that the parenchymatous tracts are narrower; in tangential section a greater difference is shown, for in *Heterangium* the fibrous strands take a straight vertical course, and only anastomose with one another at long intervals.

We have now to consider the distribution and structure of the vascular bundles which supply the leaves. The main points in their longitudinal course were determined by Williamson in his first investigation of the plant in 1872, when he examined a series of eight transverse sections from a piece of stem nearly two inches long. In this length the bases of two leaves were met with, into each of which a vascular bundle was traced. The arrangement of the leaf-traces in this specimen, as well as in others, shows that the phyllotaxis was $\frac{3}{8}$. This was probably the usual arrangement in the larger stems of *Heterangium Grievii*; in the smaller specimens a $\frac{2}{5}$ divergence is found.

The leaf-trace bundles passed out very gradually, as

in *Lyginodendron*, so that a considerable number—usually about eight—are met with in any transverse section of the stem (Figs. 154 and 155, *l.t*). They are of large size, and closely resemble the leaf-traces of *Lyginodendron*, except that they are usually without any secondary tissues. On leaving the stele the leaf-traces are collateral, but become concentric before entering the base of the leaf itself. They soon pass out from the pericycle into the cortex, and are most frequently found in the latter tissue, whereas in *Lyginodendron* they follow the pericycle for a longer distance. The trace usually remains undivided throughout its course; this, however, is only a specific character, for other forms of *Heterangium* resemble *Lyginodendron* in having twin leaf-traces.

2. *The Leaves.*—The leaf-bases are constantly found in connection with the stem, to which they give an angular form, as they are decurrent, and the sharp projection which marks the position of each leaf in the stem extends a long way down—probably to the next leaf of the same vertical series. Hence, when the phyllotaxis is $\frac{3}{8}$, the stem has eight more or less prominent angles, corresponding to the orthostichies (Figs. 154 and 159).

The structure of the petioles is well shown in those which are still attached to the stem, and the knowledge thus gained enables us to identify the free specimens with certainty. The petiole is traversed by a single vascular bundle of concentric structure. The inner cortex contains conspicuous horizontal plates of sclerotic tissue, like those of the stem, while the hypoderma

consists of the usual alternating longitudinal strands of sclerenchyma and cellular tissue. The whole structure is much like that of the petiole of *Lyginodendron oldhamium*, but the spinous emergences characteristic of the latter plant are absent.

The petiole branched freely, and the smaller ramifications of the rachis are only about one-tenth as thick as the main leaf-stalk. Thus the leaf, like that of *Lyginodendron*, was a highly compound one; remains of the leaflets are often found, but it has not as yet been possible to determine their minute structure. The evidence available, from the petrified specimens, leads to the conclusion that the foliage was of the same type, as regards both anatomy and general Sphenopterid form, as that of *Lyginodendron oldhamium*.

3. *The Roots*.—The bases of adventitious roots are often found in connection with the stem; in a specimen from the Coal-measures, belonging to *H. Lomaxii*, a species closely allied to *H. Grievii*,[1] three such roots were found together, ranged in a vertical row on the stem. They were clearly of endogenous origin, and are placed opposite one of the primary bundles of the stem. The steles of stem and root are connected by a system of oblique vascular strands, apparently of secondary origin.

Miss M. Benson, F.L.S., has recently obtained evidence as to the structure of the roots of *H. Grievii*,

[1] In the memoir by Dr. Williamson and myself ("Further Observations," etc., Part iii. *Lyginodendron* and *Heterangium*) these two species are united. It is, however, better to separate them, as there are some slight distinctive characters, and their horizons are widely apart. The name *H. Lomaxii* was suggested by Williamson in MS. for the Coal-measure form, which Mr. Lomax first found at Dulesgate.

previously unknown. She permits me to quote the following brief statement of her results: "Recently in a series of nineteen transverse sections through a single stem of *H. Grievii*, roots were found emerging from the stele and branching in the cortex, which was locally much thickened. In some sections these roots were cut transversely, and proved to be diarch or triarch. No exodermis could be distinguished from the rest of the cortex, as in *Lyginodendron*." In the case of the Coal-measure species, *H. Lomaxii*, there is some evidence that the roots were tetrarch, but proof of continuity is not yet established.

4. *Heterangium tiliaeoides*.—The other forms which have been referred to the genus *Heterangium* agree in essentials with *H. Grievii*, but there is one which deserves special notice, on account of the astonishing perfection with which its tissues are preserved. This is the *Heterangium tiliaeoides* of Williamson, first described by that author in 1887,[1] from specimens found in the Lower Coal-measures of Halifax. The general structure is like that in the species already described, and here also the entire interior of the stele is occupied by groups of tracheides interspersed with conjunctive parenchyma. The primary, mesarch xylem-strands at the periphery of the central wood, are, however, much more distinct in the Halifax species, and at once strike the eye as definite bundles, separated from one another by bands of conjunctive tissue. The

[1] "Organisation of Fossil Plants of the Coal-Measures," Part xiii., *Phil. Trans. Roy. Soc.* B, vol. 178, 1887. See also Williamson and Scott, "Further Observations," etc., Part iii., *Phil. Trans.* B, vol. 186, 1895.

secondary wood attained a considerable thickness, and is divided up into distinct groups, corresponding to the peripheral primary strands, and separated from one another by the principal medullary rays, while numerous secondary rays are also present. The bordered pits

FIG. 158.—*Heterangium tiliaeoides*. Radial section through part of secondary wood and phloëm. x^2, secondary wood; *tr'*, fully developed pitted tracheides; *tr*, tracheides with pits beginning to form; *cb*, cambium; ph^2, secondary phloëm; *sv*, sieve-tubes; *sv.p*, sieve-plate; *r*, phloëm-ray. × 112. *Phil. Trans.*, W. and S. Will. Coll. 1628.

on the tracheal walls are exquisitely preserved, and in favourable cases their development can even be traced, in the elements bordering on the cambium (Fig. 158, *tr*). The cambium itself is also perfectly preserved, but the special interest of the specimen centres in the phloëm, which is perhaps better shown

in *H. tiliaeoides* than in any other fossil plant. On entering the phloëm-zone, the principal rays become widely dilated, broadening out into conspicuous wedges, and exactly resembling the phloëm-rays of the lime-tree, a fact to which the fossil owes its specific name.

The phloëm attained a great thickness, scarcely inferior to that of the secondary wood. To the outside of each group, the primary phloëm, corresponding to the primary xylem-strand within, can be distinctly recognised. The greater part of the phloëm is secondary, and has a definite radial seriation of its elements.

The phloëm proper, as distinguished from the secondary rays which pass through it, consists of alternating bands of long parenchymatous cells, and of sieve-tubes. The latter are so perfectly preserved as to show, in some cases, the compound sieve-plates on their radial walls, closely resembling similar structures in recent Cycads. Details of this kind are necessarily among the rarities of fossil preservation (see Fig. 158 *sv.p*).[1]

Beyond the phloëm-zone is a very wide pericycle, the structure of which agrees closely with that in *Lyginodendron*, as it contains groups of stone-cells, elements which, in the case of *Heterangium Grievii*, are limited to the cortex. The pericycle in *H. tiliaeoides* also resembles *Lyginodendron* in showing the beginning of periderm-formation in its outer layers.

The cortex, which is less perfectly preserved than

[1] For details of the sieve-tubes, see Williamson and Scott, "Further Observations," etc., Part iii., Plate xxix., Figs. 38 and 38 A.

the other tissues, agrees in structure with that of the former species.

The outgoing leaf-trace bundles are nearly always found in pairs, as in *Lyginodendron*. Judging from the one instance in which a petiole has been found, in this species, in connection with the stem, it appears that the two bundles united on entering the leaf-base.

In *H. tiliaeoides*, as in the other forms, adventitious roots were borne on the stem, but we are not as yet acquainted with their detailed structure.

Apart from the exceptionally perfect preservation of its tissues, *Heterangium tiliaeoides* is of special interest from the fact that in several details—as in the distinctness of the peripheral xylem-strands of the stele, the distribution of the sclerotic elements, and the paired leaf-traces—it approaches *Lyginodendron oldhamium*, while in its general structure it retains all the essential *Heterangium* characters. The affinity of this species with *Lyginodendron* is so evident as to prove beyond reasonable doubt that the proper place of *Heterangium* is in the Lyginodendreae, rather than in the Medulloseae (see next chapter). It is also interesting to see how closely the detailed structure of the secondary tissues, in this Fern-like plant, resembled that in the recent Cycads.

5. *Habit.*—As regards the external habit of the genus *Heterangium*, we have good evidence in the case of the species *H. Grievii*. From the study of the specimens with structure preserved, we know that the plant possessed long angular stems, about a centimetre or a centimetre and a half in diameter, bearing, at

intervals of a couple of centimetres or more, large stalked leaves, with a repeatedly branched rachis, bearing numerous, finely segmented leaflets; the arrangement of the leaves on the stem was a spiral one, and the commonest divergence appears to have been $\frac{3}{8}$. Now there is a "Fern," of which the external characters are well known, which agrees in all the points mentioned with our fossil, and which is common in deposits of the same geological horizon, both in Scotland and on the Continent. This is the *Sphenopteris elegans* of Brongniart, which is represented in Figs. 159 and 160, from Stur's figures. The stem, a portion of which, slightly reduced, is shown in Fig. 159, bears the bases of several petioles, and Stur, who investigated specimens from the Culm of Bohemia, found that the phyllotaxis was $\frac{3}{8}$. The angles of the stem correspond to the orthostichies of leaves; the general aspect of the frond, which was large and of the *Diplotmema* form (*i.e.* with the primary pinnae forked), is indicated in Fig. 160.

But, besides the general resemblance in external habit, there is one character which appears decisive as to the identity of *Heterangium Grievii* with *Sphenopteris elegans*. It will be remembered that the inner cortex of *H. Grievii*, both in stem and petiole, contains numerous horizontal plates of stone-cells, giving a characteristic transverse striation to the specimens, wherever this part of the tissue is exposed to view. Now in *Sphenopteris elegans*, though only preserved in a carbonised condition, without any minute structure, precisely the same feature is shown; wherever the superficial layers had broken away from the stem or leaf-stalk, so as to expose the more internal cortical tissues,

a transverse striping is exhibited, answering exactly to the sclerotic plates of the petrified specimens

FIG. 159.—*Sphenopteris elegans* (probably = *Heterangium Grievii*). Ribbed stem, bearing several petioles. Note the transverse marks on the surface, where the inner cortex is exposed, corresponding to the sclerotic bands of *H. Grievii*, as shown, for example, in Fig. 154. $\frac{2}{3}$ nat. size. After Stur.

(see Figs. 159 and 160, and compare with Fig. 154). We may therefore, on the whole of the evidence, take it as proved that the structural specimens

known as *Heterangium Grievii* are identical with

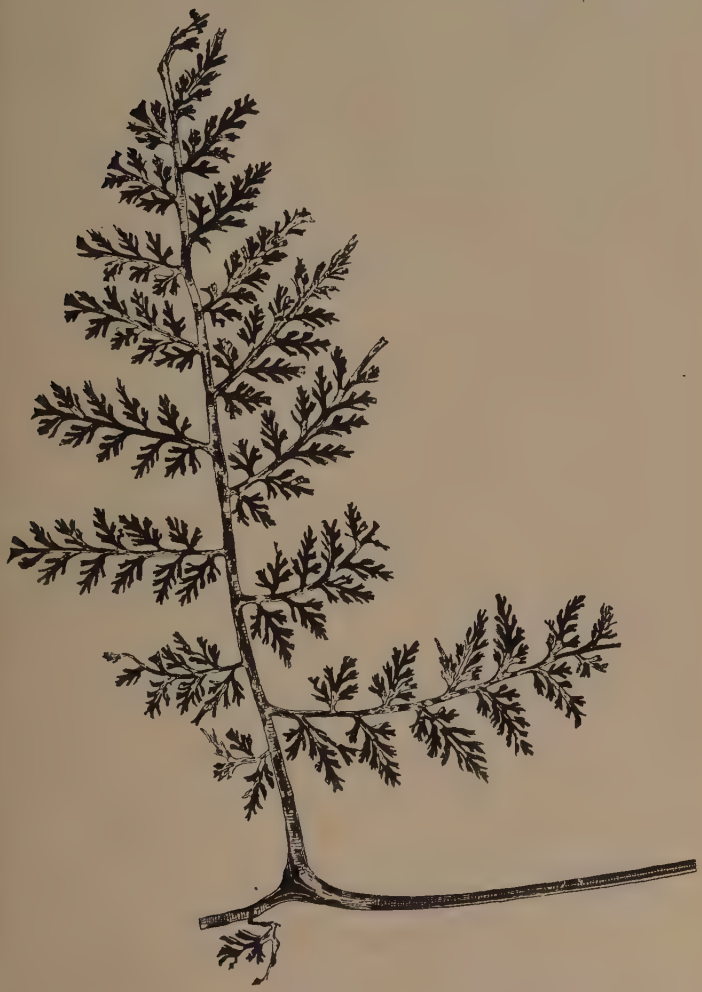

Fig. 160.—*Sphenopteris elegans* (probably foliage of *Heterangium Grievii*). Part of frond. Note the transverse bands on the rachis, as in Fig. 159. ⅔ nat. size. After Stur.

Sphenopteris elegans, Brongn., or with some closely

similar species of *Sphenopteris*. This identification was, in the first instance, due to the penetration of Mr. R. Kidston,[1] who has further pointed out to me that at least two other Lower Carboniferous fronds, *S. Linkii* (Göpp.) and *S. dissecta*, Brongn., also show characters identifying them with *Heterangium*, of which there must clearly have been several species in this Flora.

We have therefore to picture *Heterangium Grievii* to ourselves as a Fern-like plant, with a long, upright, or perhaps trailing, ribbed stem, bearing large and graceful, finely divided fronds, much resembling those of some recent *Asplenium*.[2]

III. Affinities of Lyginodendreae

At present we have no certain knowledge of the fructification of *Heterangium*; the various species of *Sphenopteris* which no doubt represent the foliage of the genus have so far only been found in the sterile condition. Associated with *Heterangium Grievii* in the Burntisland petrifactions are seeds (*Conostoma ovale* and *C. intermedium*), described by Williamson in 1876,[3] which are evidently very nearly allied to *Lagenostoma*, as shown by the structure of the testa and pollen-chamber. It is very probable that they may have belonged to *Heterangium*, but there is as yet no direct evidence. As has been shown above, the agreement

[1] Kidston, "Fructification and Internal Structure of Carboniferous Ferns," *Trans. Geol. Soc. Glasgow*, 1889, p. 49.

[2] When first discovered, the present *Sphenopteris elegans* was identified with *Fumaria officinalis*, which is thus a synonym for *Heterangium Grievii*, certainly a strange freak of nomenclature!

[3] "Organisation of Fossil Plants of Coal-measures," Part viii., *Phil. Trans. Roy. Soc.* vol. 167, p. 243, Figs. 80-87.

in the vegetative structure, including habit as well as anatomy, between *Heterangium* and *Lyginodendron* is sufficiently close to leave no doubt that they belonged to the same family, and presumably bore a similar type of fructification. Nevertheless the fact of the protostelic structure of the *Heterangium* stem, apparently so unlike anything known in other Spermophyta, will give a peculiar interest to the discovery of the reproductive organs of this genus (compare *Sutcliffia*, p. 447).

But while *Heterangium* was in all probability a Seed-plant like *Lyginodendron*, it is important to recall the points in which it shows affinity with the Ferns.

The external habit was altogether that of a Fern, so much so that no modern botanist would have hesitated in placing it, so far as these characters are concerned, among the Filices. The internal organisation to a great extent confirms this conclusion. The concentric structure of the vascular bundle in the petiole is quite Fern-like, while an even more important character, the primary structure of the stem agrees wonderfully closely with that of some of the simpler Filices. We must, of course, go to a protostelic Fern for an analogy, and it is with the simpler species of *Gleichenia* that the correspondence is closest. In most Gleichenias the single stele consists of a central mass of xylem, surrounded by a zone of phloëm. The xylem is made up of intermixed tracheides and conjunctive parenchyma, just as in *Heterangium*, and the position of the protoxylem is the same in the recent as in the fossil genus, for in both, the spiral tracheides form a number of groups a little within the periphery of the wood, of which the greater part is consequently centri-

petal, while a small portion is developed centrifugally. The phloëm-zone is surrounded by a pericycle several cells thick.

The general structure of the stele is thus very closely similar to that in *Heterangium*. The leaf-traces, one of which passes out to each leaf, are not alike in detail, and we must not push the analogy too far. The anatomical agreement between *Gleichenia* and *Heterangium* is, however, quite near enough to prove that the stem-structure of the latter genus is essentially that of a protostelic Fern, from which it differs in scarcely anything but the presence of secondary tissues, and the mode of pitting of the tracheides; the latter character, however, is common to many of the Botryopterideae.

If *Heterangium*, and especially *H. Grievii*, stood alone, we should have little reason for regarding it as anything more than a Fern, which had acquired the power of secondary growth, just as the fossil Lycopods acquired it without thereby becoming anything more than Lycopods. But even within the same genus, when we consider *H. tiliaeoides*, it is impossible not to be struck by the resemblance of the secondary tissues to those of Cycads, and by the distinctness of the peripheral strands of the wood, recalling the mesarch xylem of Cycadean foliar bundles.

When we come to *Lyginodendron*, which we know to have been a Seed-plant, the vegetative anatomy still shows many points of agreement with Ferns, though the Cycadean characters are more evident. The primary bundles are here isolated from one another, and disposed around a wide pith. The whole organi-

sation of the vascular zone, both primary and secondary, is what that of a Cycad would be if the mesarch structure of the foliar bundles were continued down from the leaves into the stem. But we now know that this is precisely what occurs in certain Cycadean peduncles, which are themselves portions of the stem.

The stem-structure of *Lyginodendron* is, in fact, as a whole rather Cycadean than Filicinean, though in the young condition, before secondary growth had set in, there is a clear analogy with such a Fern as *Osmunda*. In the form and structure of the leaf *Lyginodendron* is as Fern-like as *Heterangium*. In both genera the abundant adventitious roots are suggestive of a Fern rather than a Cycadophyte ; their anatomical structure, when young, is not unlike that of the roots of Marattiaceae, or some Ophioglossaceae, though the secondary changes soon give them a more Cycad-like character.

The discovery of the reproductive organs, while it has finally transferred the Lyginodendreae to the Spermophyta, has in one important respect emphasised their affinity with the Ferns. The male fructification *Crossotheca* and the probably allied *Telangium* described by Miss Benson bear an unmistakable resemblance to the synangia, such as those of *Scolecopteris* and *Asterotheca*, attributed to Marattiaceae, and also to those of recent Ferns of that order. Even if all the supposed Carboniferous Marattiaceae turned out to be Pteridosperms (a very improbable supposition, as shown in Chapter VIII.), the Fern-like character of the microsporangia in the latter class would only be the more significant.

A more general discussion of the affinities of Pteridosperms will follow later; as regards the Lyginodendreae it is evident that their affinities, on the Cryptogamic side, are altogether with the Ferns, though doubtless they sprang from that stock long before any of the Fern families now familiar to us had come into being. On the other hand, the near relations between the Lyginodendreae and the Cycadophyta are manifest, as shown, above all, in the structure of the seed.

The Lyginodendreae have also been named the Sphenopterideae, and there can be little doubt that a large proportion of the Fern-fronds of the *Sphenopteris* type belonged to this Pteridospermous family. If, however, we may take the *Crossotheca* type of microsporangiate organ as characteristic, the family was not limited to Sphenopterid foliage, for various species of *Crossotheca* are known to have been borne on Pecopterid fronds.[1] As regards seeds referable to Lyginodendreae, it appears certain that the various species of *Lagenostoma* and some of those in Williamson's genus *Conostoma*, so similar in all essentials to the seed of *Lyginodendron oldhamium*, must have belonged to the same group of plants. This probably also holds good for *Physostoma*, in spite of its unique peculiarities (see above, p. 396).[2]

A very remarkable fructification which may prove to have affinity with this family is that described by

[1] Three such species are enumerated by Mr. Kidston, *Microsporangia of Pteridospermeae*, *l.c.* p. 432, besides two other Pecopterids, regarded by M. Zeiller as probably belonging to *Crossotheca*. One of the latter, *Pecopteris exigua*, is especially interesting, as the structure is known, and bears considerable resemblance to that of *Telangium Scotti*. See Renault, *Cours de bot. foss.* t. iii. Plate xix. Figs. 13-18.

[2] See Prof. F. W. Oliver "On *Physostoma elegans*," *Ann. of Bot.* vol. xxiii. January 1909.

Renault under the name of *Gnetopsis elliptica*,[1] from the Permo-Carboniferous of St. Étienne. In this case four seeds (of which two are often abortive) are enclosed within a common envelope or cupule, consisting of two partly fused bracts, each of which is divided into about five teeth above, and traversed by the same number of vascular bundles. The seeds or ovules are small (2.5 mm. long) and have a remarkable structure. The integument, which is traversed by four vascular strands, expands around the micropyle into a chambered or lacunar region, comparable to the canopy of *Lagenostoma*, and bears two long feathery appendages. M. Renault ingeniously suggested that the seed was thus adapted to transport either by water or wind. The pollen-chamber appears to have a central column as in *Lagenostoma*, while the neck of the chamber is divided into lobes. The endosperm and the two archegonia are preserved. In several points—the structure of the pollen-chamber and integument and the presence of a cupule—there are thus decided analogies with the seed of *Lyginodendron*, though the differences are no less marked. An affinity with the Lyginodendreae certainly seems more probable, in the present state of our knowledge, than that with the Gnetaceae, originally suggested by the discoverer.

Our knowledge of the Lyginodendreae is far too fragmentary at present for it to be possible to frame the essential character of the family. The following points may be mentioned as likely to occur in members of the group:

[1] *Cours de Bot. foss.* t. iv. 1885, p. 179; Plate xx., Plate xxi. Figs. 1-6, Plate xxi. Figs. 2-4.

Leaves filicoid (Sphenopterid or Pecopterid).

Stem monostelic; leaf-trace and main foliar bundle single or double, concentric in the petiole. Xylem mesarch.

Reproductive organs borne on somewhat modified pinnae of the frond.

Microsporangiate organs of the *Crossotheca* type.

Seeds with radial symmetry, of Cycadean type, with nucellus adherent to integument, and with a single vascular system. Seed or seeds often enclosed in a cupule.

The relations of the Lyginodendreae to other groups will be further discussed at a later stage.

CHAPTER XI

PTERIDOSPERMEAE—*continued*

Medulloseae; Aneimiteae; Seed-bearing Pecopterideae; Other Cycadofilices

MEDULLOSEAE

Habit.—As long ago as 1883 the Austrian palæobotanist Stur, as already mentioned, proposed to exclude certain of the principal genera of fossil Fern-like fronds from the Ferns, on the ground that, in spite of all the research devoted to them, they had never been found to bear Filicinean fructifications. The genera which he specially cited were *Neuropteris*, *Alethopteris*, *Odontopteris*, and *Dictyopteris*; these genera, along with others, are now often grouped in the family *Neuropterideae*, based on external characters, corresponding in part, if not altogether, to the Medulloseae as defined by structure. Recent investigation has fully justified Stur's conclusion (though not accepted at the time), and, as we shall see, there is now every reason to believe that the Neuropterideae generally were seed-bearing plants (Pteridosperms) and not Ferns. Among the genera in question *Neuropteris* and *Alethopteris*

are the most extensive and, at present, the best investigated.

The leaves of *Neuropteris* are of a very large size, bipinnate, tripinnate, or even quadripinnate in composition, with ovate or oblong leaflets somewhat

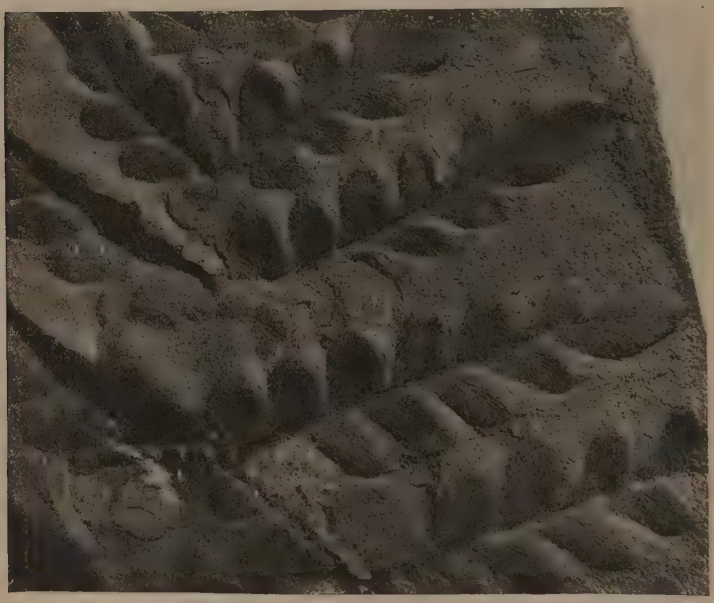

Fig. 161.—*Neuropteris heterophylla.* Part of vegetative frond, slightly enlarged. From a photograph by Mr. R. Kidston, F.R.S.

cordate at the base, and usually attached to the rachis by a short stalk. The median nerve of the pinnule is distinct till near the end, where it breaks up into smaller dichotomous nervules; similar nervules are given off from the sides of the median nerve throughout its length; they leave the latter at an acute angle, and bend outwards to the margin (Fig. 161). The fronds recall those of some recent Osmundas.

In some cases, pinnae of a different form, without a median nerve, and described under the name of *Cyclopteris*, were attached directly to the rachis, and may have been of a stipellar nature. These organs are of the same kind as the "Aphlebiae," mentioned in Chapter VIII. as occurring on the fronds of Ferns.

In the genus *Alethopteris* the leaves are likewise large, and bi- to tripinnate, but here the thick, usually oblong pinnules are inserted on the rachis by a broad, decurrent base, and are in some cases confluent with one another. The edges of each leaflet are incurved on the lower side. The median nerve extends the whole length of the pinnule, and is prominent on its under surface; the secondary nerves leave the median one at a wide angle, and pass directly, with or without dichotomy, to the margin (see Fig. 162). The habit resembles that of the recent Marattiaceous Fern *Angiopteris*.

Fig. 162.—*Alethopteris lonchitica* (foliage of a *Medullosa*). Part of frond. Reduced. From a photograph by Mr. W. Hemingway.

In the case of both these so-called genera, founded on the external characters of the leaf, there is now good evidence that they belonged to stems of the family *Medulloseae*, of which the structural characters

are known. The nature of the proof will be given later, after describing the anatomy of the stem, but while considering this, it is necessary to bear in mind that we are dealing with plants which possessed a highly compound Fern-like foliage, and which, in some forms, at any rate, must have had a habit not unlike that of some of the existing Tree-ferns. We will first describe the anatomy of various representatives of the family, beginning with the type genus *Medullosa*, and will then go on to the evidence which we now possess as to the reproductive organs, especially the seeds.

Anatomy—Medullosa.—The anatomical description will be based, in the first instance, on a British species, which is of greater geological antiquity than most other known members of the genus, and is likewise simpler in structure. As this form is now known with a considerable degree of completeness, it will best serve to give an idea of the essential anatomical characters of the group.

Medullosa anglica is derived from the Lower Coal-measures of Lancashire, at the same horizon to which most of our British Coal-plants, with structure preserved, belong. The original specimens were found in nodules from the coal-seam at the Hough Hill Colliery, Stalybridge, at dates ranging from 1892 to 1898, by the late Mr. G. Wild and Mr. Lomax.[1] It is a curious fact that these specimens were the first stems of a *Medullosa* to be found in this country, though the petioles of plants belonging to this genus had long been familiar among

[1] For a fuller description, see my paper, "Structure and Affinities of Fossil Plants from the Palæozoic Rocks, iii. *Medullosa anglica*, a New Representative of the Cycadofilices," *Phil. Trans.* vol. 191, B, 1899.

the common objects of the calcareous nodules. Specimens have since been found in other localities, and it is interesting that at Shore Littleburgh they occur in the roof-nodules, which usually show a distinct Flora from that of the nodules in the seam below.[1]

The stems are of rather large size, having a mean diameter of 7 or 8 cm., in the specimens at present known. This dimension includes the leaf-bases, which were adherent to the stem for a long distance before becoming free; in fact, practically the whole external surface was formed by these leaf-bases, which were spirally arranged, the phyllotaxis, where it could be determined, having followed the $\frac{2}{5}$ arrangement. Fig. 163 will give an idea of the external appearance of the fossil stem; the surface of the large adherent leaf-bases is marked by a longitudinal striation, due to the hypodermal ribs of sclerenchyma, which stand out prominently in the fossil, though during life they must have been nearly or quite concealed from view by overlying tissue. The transverse section, represented somewhat diagrammatically in Fig. 164, shows the chief points in the organisation of the stem. This section was cut near the bottom of a piece of stem about a foot long. At this level, three large leaf-bases are shown; that marked *c* in the figure is the nearest to its separation from the stem, and actually became free an inch or two higher up. The next leaf to become free is that marked *b*, while *a* remains in connection with the stem for a vertical distance of 5 or 6 inches. At

[1] Mr. Arber described in 1903 a specimen in the Binney Collection at Cambridge. This must have been discovered many years before the type-specimens, but had apparently lain unnoticed. See Arber, "On the Roots of *Medullosa anglica*," *Ann. of Bot.* vol. xvii. 1903.

higher levels, two new leaf-bases make their appearance, the first (*bc*) between *b* and *c*, and the next (*ab*) between *a* and *b*. Thus the order of insertion of the leaves from below upwards was *c*, *b*, *a*, *bc*, *ab*, an arrangement which implies a $\frac{2}{5}$ phyllotaxis. The habit of the stem,

FIG. 163.—*Medullosa anglica*. External view of stem, showing two large leaf-bases, with a furrow between them. The surface is ribbed, owing to the presence of hypodermal strands of sclerenchyma. $\frac{2}{5}$ nat. size. S. Coll. (G. T. G.)

clothed with its large adherent leaf-stalks, may well have resembled that of some of the Tree-ferns.

Coming now to the internal structure of the stem, we find that its organisation resembles that of the majority of the Ferns, in being of the so-called *polystelic* type.[1] The number of the steles in *M. anglica* is

[1] I have adhered to the now familiar terms "polystely" and "polystelic," but they are used in a purely descriptive sense without any implication that each of the several steles is to be regarded as homologous with the single stele of a typical monostelic stem.

normally three (see Fig. 164, *st*) ; each has a somewhat elongated and irregular transverse section ; traced longitudinally, they divide and again fuse with one another at long intervals. The structure of the individual stele is almost identical with that of the single vascular cylinder of a *Heterangium*. The central part of each stele is completely occupied by the primary wood, consisting of groups of tracheides intermixed with

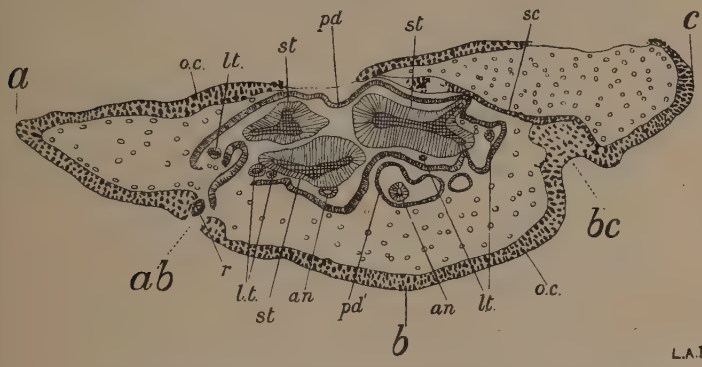

FIG. 164.—*Medullosa anglica*. Transverse section of stem, showing three large leaf-bases, *a*, *b*, and *c*. *ab*, *bc*, position of next leaf-bases above. *st*, the three steles ; *l.t*, leaf-traces ; *an*, accessory rings of wood and bast ; *pd*, periderm, forming a ring round the group of steles, and also enclosing one of the accessory strands ; *r*, adventitious root ; *o.c*, hypoderma ; *sc*, sclerenchymatous band between leaf-base and stem. Slightly reduced. *Phil. Trans.*, S. S. Coll. 737.

conjunctive parenchyma. The primary tracheides are for the most part pitted, just as in *Heterangium* ; the spiral tracheides of the protoxylem, accompanied by a few scalariform or reticulated elements, occur in several groups near the outer margin of the primary wood (see Fig. 165, which includes parts of two steles).

Each stele is surrounded separately by its own zone of secondary wood and bast (Figs. 164 and 165, x^2, *ph*), so that we have in this family a combination of polystelic

structure with normal secondary growth of the individual stele. This is the great anatomical character of the genus *Medullosa*, with its immediate allies, and separates them at once from all plants now living, though there

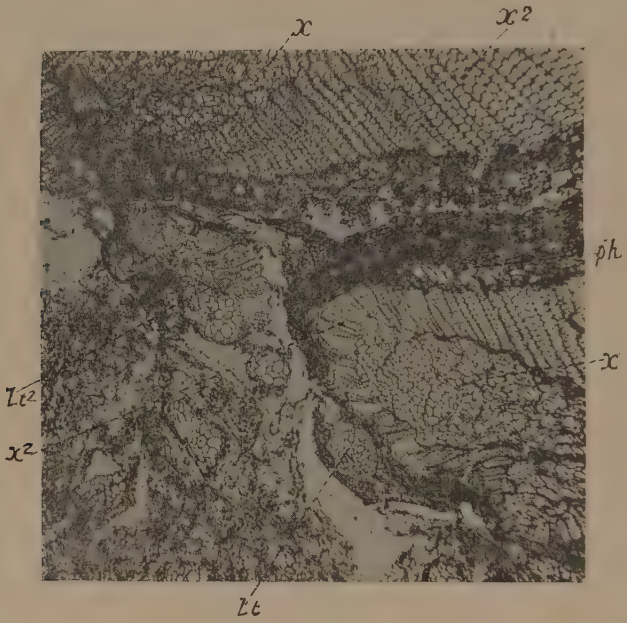

FIG. 165.—*Medullosa anglica*. Part of transverse section, showing portions of two steles, and leaf-traces going off from them. *x*, primary wood of steles; x^2, secondary wood; *ph*, phloëm; *l.t*, leaf-trace, just detached from its stele; $l.t^2$, large leaf-trace, beginning to divide. Other smaller bundles are shown. × 10. *Phil. Trans.*, S. From a photograph. S. Coll. 579.

is one other fossil family (that of the Cladoxyleae) which shares the peculiarity (see p. 496.)

The secondary wood has the same structure as in *Heterangium* or *Lyginodendron* (see Fig. 165). The tracheides, which are in radial series, accompanied by muriform medullary rays, are, as a rule, pitted on their radial walls only The pits are multiseriate and

bordered, just as in the genera last mentioned. Only slight remnants of the cambium are preserved, but sufficient to show that it was in the normal position, forming wood internally and phloëm externally, with reference to each stele. The phloëm itself is fairly preserved in places (Fig. 165, *ph*), and consisted of strands of long tapering elements, clearly the sieve-tubes, forming a network, the meshes of which were occupied by the rather wide phloëm-rays. In the Binney specimen, described by Mr. Arber, the sieve-tubes are perfectly preserved, and have conspicuous sieve-plates on their lateral walls, just as in *Heterangium tiliaeoides*.[1] There appears to have been a pericycle around each stele, but its structure is ill-preserved.

So far, the general organisation of *Medullosa anglica* may be roughly described as that of a polystelic *Heterangium*. In the points which remain to be described, the *Heterangium* type is departed from more widely; the differences are partly correlated with the polystely, and partly depend on the greater size and complexity of the plant as a whole.

The leaf-trace bundles were given off, for obvious reasons, only from the free, peripheral side of the steles. Where a leaf-trace first becomes free from the stele, it is a large bundle, to all appearance truly concentric in structure (see Fig. 165, *l.t*). It consists of a central mass of primary wood, with one or more protoxylem-groups near its external margin. This is surrounded by a zone of secondary wood and phloëm. The primary wood of the leaf-trace is continuous with the outer part of that of the stele from which it springs.

[1] Arber, *loc. cit.* Plate xx. Fig. 4.

As the leaf-trace passes upwards and outwards through the cortex, it loses its secondary tissues, and divides up repeatedly (Fig. 165, $l.t^2$) to form a number of smaller bundles, each of which eventually assumes a collateral structure. These ultimate leaf-trace bundles have their protoxylem directed outwards, adjoining the phloëm (see Fig. 166, in which two exceptionally well-preserved

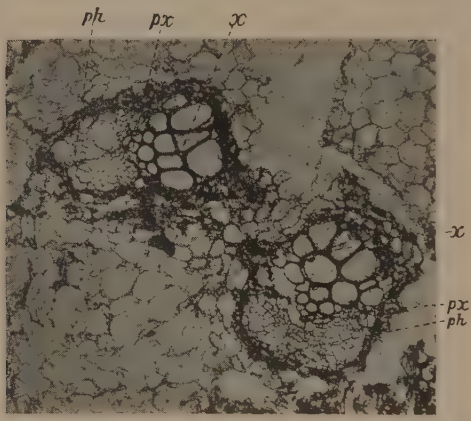

FIG. 166.—*Medullosa anglica*. Two leaf-trace bundles from the outer cortex of the stem, in transverse section, showing collateral exarch structure. *px*, protoxylem; *x*, centripetal xylem; *ph*, phloëm. × 35. *Phil. Trans.* S. From a photograph. S. Coll. 579.

collateral bundles are shown); their xylem usually consists of spiral and finely scalariform elements only, the pitted tracheides, which are abundant in the undivided leaf-traces, disappearing as the ramification of the bundle goes on.

The cortical tissues of the stem require no detailed description; they consist of short-celled parenchyma, traversed by numerous secretory canals, much resembling the gum-canals of recent Cycads.

A zone of internal periderm was formed around the central part of the stem, enclosing the group of steles, and separating them from the outer cortex and leaf-bases (Fig. 164, *pd*). The periderm was probably for the most part of a suberous nature ; it is extremely well preserved, and was evidently formed wholly or chiefly on the external side of the phellogen.

In one specimen, apparently forming part of an old stem, the whole of the outer cortex, together with the leaf-bases, had been exfoliated, leaving the periderm exposed. It may be doubted, however, whether this exfoliation was a normal process.

A point of some anatomical interest is the occasional presence, in the cortex, of accessory vascular strands, of concentric structure, and probably of wholly secondary origin (Fig. 164, *an*). These formations recall the similar cortical bundles occurring in the genus *Cycas* and some other members of the Cycadaceae at the present day.

The petioles of *Medullosa anglica* were of large size, having a diameter of 4 cm. or more, at the point where they became free from the stem. Each leaf-stalk received a large number of vascular bundles, as many as seventy or eighty in all, derived from the repeated ramification of several of the principal leaf-traces. The supply of bundles did not all enter the leaf-base from the stem at the same level ; they passed in successively, in groups corresponding to the various principal leaf-traces from which they were derived. Thus their number, in the leaf-base, increased from below upwards. At a certain height, however, the leaf-base was marked off from the interior of the stem by a band of internal sclerenchyma,

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and above this level no more bundles were received (see Fig. 164, *C*). The petiole, where it first detaches itself

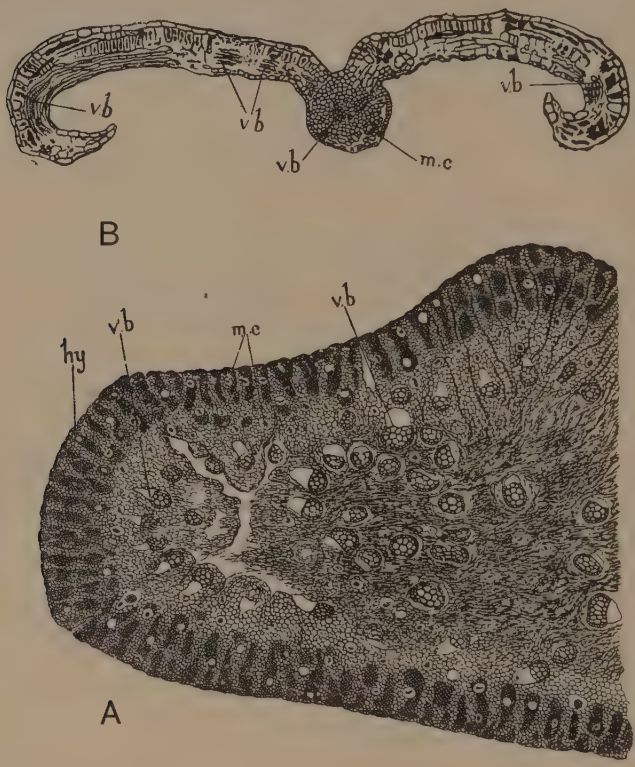

FIG. 167.—*Medullosa anglica*. A. Transverse section of petiole, showing the numerous vascular bundles, *v.b*; *m.c*, mucilage-canals; *hy*, hypoderma, with sclerenchymatous ribs. The whole has the structure of "*Myeloxylon Landriotii*." × about 8. S. Coll. 686. (G. T. G.) B. Vertical section of leaflet. *v.b*, vascular bundles of mid-rib, and lamina; *m.c.*, mucilage-canal. Palisade-tissue shown towards upper surface. × 28. *Phil. Trans.* S. S. Coll. 691.

from the stem, has the following structure (Fig. 167, A): On the extreme outside we may find a layer or two of palisade-like tissue (rarely preserved), which probably served for assimilation. Within this is the broad hypo-

dermal zone (*hy*), consisting of numerous vertical strands of fibres, interspersed with parenchyma, and accompanied by secretory canals of the usual Cycadean type.

The whole interior of the leaf-stalk is occupied by a short-celled ground-tissue, containing secretory canals (*m.c*), and traversed by the numerous vascular bundles (*v.b*), ranged more or less regularly in concentric circles. The general structure was, in fact, much like that of the petiole of a recent Cycad. The individual bundles likewise resemble those of the recent family, differing only in the fact that their xylem was entirely centripetal, while in a modern Cycad a small amount of centrifugal wood is also present. This difference, however, does not seem to have been an absolutely constant one, for in some of the Medulloseae the foliar bundles are described as having precisely the Cycadean structure.

Petioles of the kind described have long been known under the generic name of *Myeloxylon*; the particular form belonging to our *Medullosa* resembles that named by M. Renault *Myeloxylon Landriotii*, distinguished chiefly by the multiseriate arrangement and elliptical transverse section of the fibrous hypodermal strands. The same petiolar structure, however, was no doubt common to certain other species of *Medullosa*. The fact that the fossils named *Myeloxylon* are nothing but the petioles of *Medullosa* had previously been proved, by Weber and others, for one of the Continental species.[1] In the case of *M. anglica* the conclusion is perfectly obvious,

[1] See Weber and Sterzel, *Beiträge z. Kenntniss der Medulloseae*, Chemnitz, 1896. The original discovery was made by Weber, about the year 1880.

for the leaf-bases, still attached to the stem, show in all respects the typical *Myeloxylon* structure. The genus *Myeloxylon* is therefore one of those which can now be dispensed with, or at most be retained, as a matter of convenience, for those petioles which have not yet been referred to their particular species of *Medullosa*.

The petioles of *Medullosa anglica* were of great length, and branched repeatedly, the successive branches diminishing in size, and undergoing some simplification in structure. The whole evidently constituted the rachis of a highly compound, probably bi- or tripinnate leaf. The final ramifications, which are no more than a millimetre in diameter, contain only a very few vascular bundles, but these still retain the same collateral, exarch structure as those of the main petiole. Gum-canals occur throughout the rachis; the hypodermal structure becomes simplified in the finer branches, consisting of an almost continuous zone of peripheral sclerenchyma.

Associated with the branched rachis, leaflets of characteristic structure are found. As shown by transverse sections, these leaflets are constantly revolute at their margins (see Fig. 167, B); the parenchyma towards the upper surface is of palisade-like structure, while the lower portion of the mesophyll is more lacunar. The lateral bundles, which traverse the lamina in an oblique direction, are accompanied by fibrous elements. The midrib is very prominent on the lower surface, and shows the same structure as a small branch of the rachis. From constant association and agreement in structural details, there is no doubt that these pinnules formed part of the *Medullosa* leaves. This conclusion is of great interest, because the pinnules in question

agree closely with certain leaflets described by M. Renault in 1883, which, as shown by their external characters, belonged to an *Alethopteris*.[1] The rachis and petiole of M. Renault's *Alethopteris* showed the anatomical structure of "*Myeloxylon Landriotii*." Thus the French author's observations, taken in conjunction with Weber's discovery that "*Myeloxylon Landriotii*" was the leaf-stalk of a *Medullosa*, proved that the well-known *Alethopteris* fronds were borne as foliage on certain of the *Medullosa* stems.

From the organisation of the petioles and leaves in *Medullosa anglica*, there can be little doubt that the English species also bore foliage of the *Alethopteris* type, an example of which is illustrated in Fig. 162 from *A. lonchitica*, very probably the actual species concerned.

The *roots* of *M. anglica* have frequently been found in connection with the stem, on which they were borne in vertical series, between the leaf-bases. They have a normal triarch structure, and, with increasing age, formed a large amount of secondary wood and bast, interrupted opposite the protoxylem-angles by large medullary rays, just as in recent roots with secondary growth. The detailed structure of the xylem agrees with that of the corresponding tissue in the stem. Mr. Arber finds that the phloëm much resembles that in the stem of *Heterangium tiliaeoides*. The groups of sieve-tubes are accompanied by phloëm-parenchyma, and separated by dilated parenchymatous rays. The sieve-tubes show the lateral sieve-plates particularly well;[2]

[1] Renault, *Cours de Botanique fossile*, vol. iii. p. 159, Plate xxvii.

[2] Arber, *loc. cit.* Plate xx. Fig. 5.

this appears to be the only case in which this structure has been recognised in the root of a fossil plant. A very characteristic feature of these roots, with the exception of the youngest specimens, is the presence of a wide zone of large-celled periderm, forming the external covering of the organ. Developmental stages have been observed, proving that the periderm was an internal one in origin, arising by division of the pericyclic cells, and thus causing the exfoliation of the whole cortex. A small amount of phelloderm was formed on the inner side of the cork-cambium.[1] In all respects the roots of *Medullosa anglica* agree with those of recent Gymnosperms.

The larger roots reached a diameter of about half an inch. They branched pretty freely, giving off rootlets of various orders. The xylem of the rootlet was always inserted on an angle of the primary wood of the main root, in the way normal for these organs.

If we now sum up our knowledge of the vegetative organs of *Medullosa anglica*, we find that it had a polystelic stem, each of the steles, usually three in number, resembling, as regards both the primary and secondary tissues, the single central cylinder of a *Heterangium*.

Externally, the stem was clothed by the bases of the large, spirally disposed leaves, which were repeatedly compound, and no doubt presented the external characters of an *Alethopteris*, with which they agree in anatomical structure.

Each leaf received from the stem a large number of vascular bundles, derived from the repeated subdivision

[1] Arber, *loc. cit.* p. 428, Plate xx. Fig. 2.

of a number of the principal leaf-traces springing from the steles. The principal leaf-traces were concentric in structure, and surrounded by secondary wood and bast, but, as the bundle underwent subdivision, its branches gradually lost their secondary tissues, and, at the same time, assumed a collateral, exarch structure. The petiole and rachis had in all respects the structure of "*Myeloxylon Landriotii*." The stem bore triarch, adventitious roots, forming secondary wood and bast, and coated by a periderm of pericyclic origin.

The form of *Medullosa* just described, which happens to be the one most completely known up to the present time, represents the genus, as it were, in its simplest expression.[1] Several Continental species had previously been investigated, all of which are of later geological age than *M. anglica*, belonging chiefly to the Permian beds. They all have a more complex vascular system than the English species; the steles are usually more numerous, and in all cases show a differentiation among themselves. The larger steles are associated to form a single or double peripheral ring, while others, of much smaller size, are grouped in the central region of the stem. In most of the specimens, as, for example, in those of the form known as *Medullosa stellata*, the peripheral steles are few in number, and much elongated in the tangential direction, so that they collectively

[1] A very small *Medullosa* (named provisionally *M. pusilla*), the stem with the leaf-bases not exceeding 2 cm. in diameter, has since been found by Mr. P. Whalley of Colne, Lancs. The stem has three steles and agrees very closely with *M. anglica* except in size. In the Renault collection at Paris there are sections, under the name *Heterangium geriense*, of the stem of a *Medullosa*, apparently of the same type as *M. anglica*, from the Upper Coal-measures of the Ride de Gier, near St. Étienne. This species may bear the name *Medullosa geriensis*.

form an almost continuous ring, with few interruptions. In some cases the peripheral ring appears to have been completely unbroken, forming a solenostele, such as we find in various recent Ferns and Fern-allies, as, for example, in *Loxsoma*, *Dicksonia*, and *Marsilia*. In all cases, however, so far as satisfactory investigations have been made, the structure of the individual stele is essentially like that in *Medullosa anglica*. The interior is occupied by primary wood, sometimes containing a rather large amount of parenchyma, and this is surrounded on all sides by secondary wood and phloëm. The small central steles usually have an approximately circular transverse section; they anastomose both among themselves and with the peripheral steles, which they resemble in structure. We see, then, that in all these forms of *Medullosa*, the structure of the stem was polystelic, as in the simpler species, *M. anglica*, with which we started. The differentiation of the steles into a central and peripheral system marks, however, a distinct advance on the part of the later representatives of the genus. The outer, more or less continuous, stelar zone allowed of indefinite growth in thickness, on its free external side. It is the rule, in the older stems of the type of *Medullosa stellata*, to find that the great bulk of secondary wood and bast was developed on the outer side of the peripheral steles; on the inner side of the same zone, and around the small central steles, the growth was of necessity limited by want of space. Consequently, an old stem of *Medullosa stellata* may assume a very different appearance, as seen in transverse section, from that typical of the genus, the external wood and bast predominating so largely over all the

other tissues, that the original polystelic organisation sinks, as it were, into the background.

In some exceptional instances, additional complications made their appearance. This was the case, for example, in a huge specimen of *Medullosa stellata* (var. *gigantea*), the largest as yet discovered, the stem of which, though decorticated, was over a foot and a half thick. The central ground-tissue, 5 or 6 inches in diameter, was traversed by forty-three central steles, some of which were an inch in diameter. The peripheral zone of steles was enormously thickened on its outer surface, but, in addition to this, there were three concentric extrafascicular layers of wood and bast, which had been formed successively around the whole of the normal vascular system. Thus, in this specimen, the anomaly characteristic of the recent Cycadean genera, *Cycas*, *Macrozamia*, and *Encephalartos*, co-existed with the polystelic structure of a *Medullosa*.[1]

It is evident that some of the Permian Medulloseae reached the dimensions of fair-sized trees; others appear to have had long and comparatively slender stems; it has been conjectured that some of the latter may have been climbers, like the lianes of tropical forests, but for this supposition there is no real evidence. The resemblance of the anatomical structure of the Medulloseae to that of the stems of certain climbing Sapindaceae, pointed out in 1881 by Göppert and Stenzel,[2] is more apparent than real. Some of the Sapindaceous lianes have a number of vascular cylinders in the mature stem, but this is merely an anomaly of

[1] See Weber and Sterzel, *l.c.*

[2] "Die Medulloseae, eine neue Gruppe der fossilen Cycadeen," *Palæontographica*, 1881.

secondary growth, depending on the peculiar distribution of the cambium ;[1] the whole structure is no doubt an adaptation to a climbing habit. In *Medullosa* the primary organisation was evidently polystelic (dialystelic), as in most recent Ferns, and there is no reason to assume that it had any relation to scandent growth.

It may be pointed out here that the polystely of *Medullosa* differs from that of the typical polystelic or dictyostelic Ferns in having, so far as appears, no relation to the presence of "leaf-gaps." In the species at present investigated the leaf-traces of *Medullosa* are given off from the outer faces of the steles, and leave no gaps ; the breaking up of the original stele depended on some other cause. Further investigation is necessary to show whether this distinction is absolute.

In one or two of the Continental Medulloseae, something has been ascertained as to the course of the leaf-traces ; thus, in *M. stellata*, the leaf-traces are given off from the peripheral steles, and each is at first surrounded by its own zone of secondary wood. They then divide up, lose their secondary tissues, and become collateral, just as in *M. anglica*. They have not, however, been traced into the leaves, which are as yet unknown in *M. stellata*.

In another Continental species, *M. Leuckarti*,[2] the leaf-traces behave in the same way, though their connection with the steles appears not to have been seen at present. In *M. Leuckarti* the structure of the leaf-bases is known, and, as in the English species, is of the type of "*Myeloxylon Landriotii*."

[1] Cf. De Bary, *Comparative Anatomy of Phanerogams and Ferns*, English edition, 1884, p. 581.

[2] Solms-Laubach, "Ueber *Medullosa Leuckarti*," *Bot. Zeitung*, 1897.

In both the species of *Medullosa* just mentioned, the leaf-traces are given off from the outermost steles. In *M. Solmsii*, however, where there is a double zone of peripheral steles, it appears that the bundles arise from the inner ring. In no case were the more central cylindrical steles directly connected with the leaf-traces, though there was indirect communication, by means of fusions with the peripheral system.

Our knowledge of the foliage of the Continental *Medullosae* is a matter of inference. *M. Leuckarti*, as already mentioned, bore leaf-stalks with the structure of "*Myeloxylon Landriotii*," and we know, from M. Renault's researches, that petioles with that structure belonged to *Alethopteris*. There is therefore a strong presumption that the foliage of *Medullosa Leuckarti*, like that of *M. anglica*, was of the *Alethopteris* type. *M. Leuckarti* seems to have had a short stem, and may have been of almost herbaceous habit. From the structure of the leaf-traces in *M. stellata*, which includes the largest specimens of the genus, there is little doubt that its petioles were also of the "*Myeloxylon*" kind, but we have no more direct evidence as to the nature of the leaf.

"*Myeloxylon*" petioles, of the type named by M. Renault *M. radiatum*, characterised by the radially elongated hypodermal bands of sclerenchyma, were shown by him to belong to the genus *Neuropteris*. There is therefore strong evidence that the latter genus, as well as *Alethopteris*, consisted, wholly or in part, of the foliage of species of *Medullosa*. Fern-like leaves of certain other genera, such as *Odontopteris*, *Callipteris*,

and *Taeniopteris*, have been found in association with stems of the same type.

A curious fossil stem, from the Permian of Autun, in France, named by Brongniart *Colpoxylon aeduense*, and subsequently more fully described by M. Renault,[1] agrees in many respects with the simpler forms of *Medullosa*, but is peculiar in having, for a part of its length, a single vascular cylinder only. The stele has a very irregular outline, and is surrounded by secondary wood and bast of the structure usual in Medulloseae. In the interior there are scattered groups of tracheae, embedded in parenchymatous tissue.

Towards one end of the specimen, the stele divides, first into two, and then into six or seven parts, so that the stem of *Colpoxylon* was monostelic in one part, and polystelic in another. The leaf-trace bundles are preserved, and appear to agree essentially with those of *Medullosa*. Their ultimate branches are collateral, and of the "*Myeloxylon*" type; in some of them, centrifugal as well as centripetal wood has been found. The external surface of the stem bears a general resemblance to that of *Medullosa anglica*; the leaves are unknown. There can be no doubt that *Colpoxylon* belonged to the family Medulloseae; very possibly it may ultimately prove to have been simply an aberrant representative of the genus *Medullosa* itself. The local reduction of the vascular system of the stem to a single stele is the point of chief interest. There is some evidence that *Colpoxylon* was the stem of an *Alethopteris*.[2]

[1] *Flore fossile d'Autun et d'Epinac*, Part ii.

[2] Grand'Eury, "Sur les organes et le mode de végétation des Neuroptéridées et autres Ptéridospermes," *Comptes Rendus*, t. cxlvi. p. 1243, 1908.

Sutcliffia.—Professor Seward described, under the name of *Rachiopteris Williamsoni*,[1] a petiole which bears a great general resemblance to "*Myeloxylon*," but differs from it (among other minor points) in the vascular bundles having concentric, instead of collateral structure. Considering that in *Medullosa* the leaf-traces were, to all appearance, concentric on first leaving the steles, it was not surprising that in some forms they should have retained this structure after entering the petiole, and it thus appeared from the first highly probable that *Rachiopteris Williamsoni* represented the leaf-stalk of some unknown member of the Medulloseae.

This conclusion has now been confirmed by the discovery of a new Medullosean stem (*Sutcliffia insignis*, Scott), found by Mr. J. Lomax in material from Mr. Sutcliffe's colliery at Shore, Lancashire.[2] *Sutcliffia*, like Professor Seward's fossil, is derived from the roof-nodules, where it is associated with Goniatite shells (Fig. 168). The roof-nodule specimens no doubt represent the drifted fragments of a distinct Flora, flourishing at some little distance from the coal-forming forests; to the latter the ordinary seam-nodules owed their origin.

The stem is a large one, measuring 12 × 6.5 cm. in diameter in its present somewhat distorted condition. In a length of 9 inches not more than one petiole leaves the stem, so the plant was presumably of a tall stature. The stem is clothed by large, spirally-arranged leaf-bases, but detached petioles have been found greatly exceeding in size those borne by the

[1] *Annals of Botany*, vol. viii. 1894, p. 287.

[2] Scott, "On *Sutcliffia insignis*, a New Type of Medulloseae from the Lower Coal-measures," *Trans. Linn. Soc. London*, 2nd ser. Bot. vol. vii. Part iv. 1906.

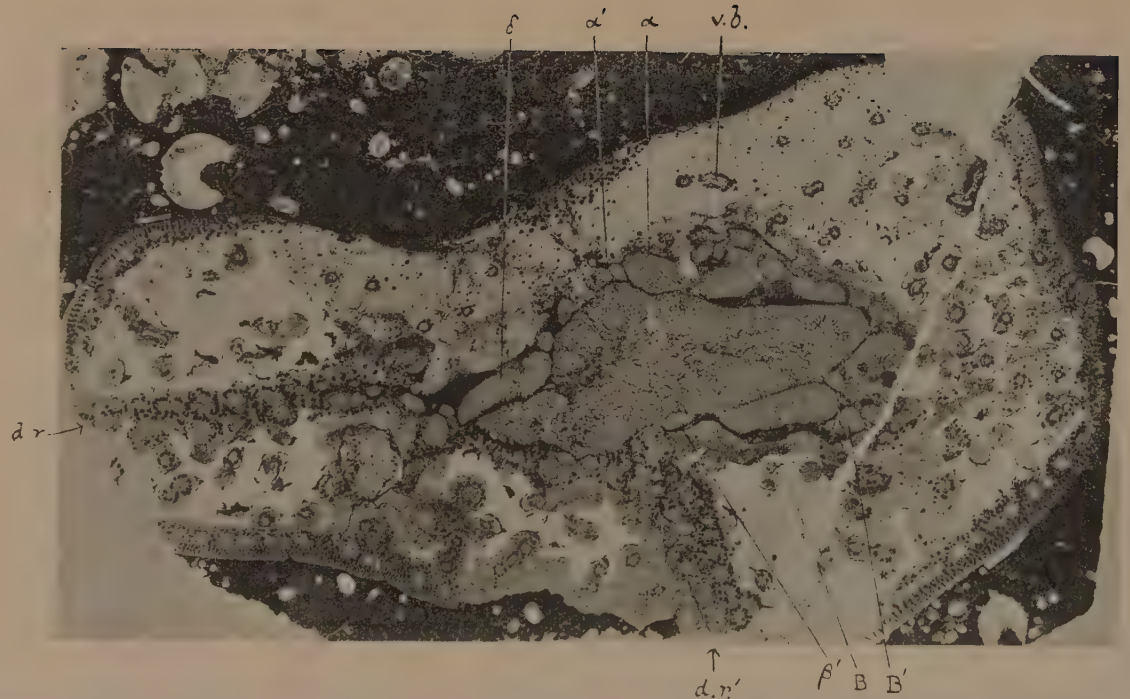

FIG. 168.—*Sutcliffia insignis*. Transverse section of the stem and leaf-bases. At α, δ, and other places, meristeles are seen separating from the central stele. B, fused mass derived from two meristeles; B′, strand branching off from B; β′, a strand previously detached; α′, two bundles derived from the meristele α; *v.b*, two leaf-trace bundles fusing; *d.r*, *d.r′*, double row of bundles probably marking the line along which a petiole will separate, higher up the stem. Very slightly enlarged. From a photograph by Mr. L. A. Boodle. Section lent by Professor F. E. Weiss.

stem, which must have been a small specimen—probably from a young plant.

The main feature of the anatomy, in which *Sutcliffia* differs from any Medullosean stem previously known, is the presence of a single central stele, of large size (measuring 4.7 × 1.8 cm. in the section figured, Fig. 168). There is no pith, and the wood has the same structure as in a stele of *Medullosa anglica*, except that in *Sutcliffia* the protoxylem-groups are peripheral, the xylem thus being exarch. A zone of phloëm, in which strands of sieve-tubes can be recognised, surrounds the wood. In the stem investigated (the only specimen as yet discovered) secondary growth was just beginning.

From the main stele, large, irregular strands, the meristeles or subsidiary steles, were detached at intervals, giving a remarkable and unique appearance to the transverse sections (see Fig. 168, *a*, B, and *δ*). The meristeles break up into smaller strands, but the main branches of adjacent meristeles often fuse with one another. Thus the large mass B, in Fig. 168, is the product of such a fusion, as shown by the comparison of serial sections. The strands derived from the further subdivision of the meristeles or their fused branches (Fig. 168, *α′*, *β′*, B′) ultimately constitute the numerous bundles of the leaf-trace (Fig. 168, *d.r.*, *v.b.*). The vascular strands in the leaf-bases and petioles always, however, retain a concentric structure, and their xylem contains parenchyma, so that they preserve a more stele-like character than the corresponding bundles in a *Medullosa*. The structure of the petiole agrees in all essentials, though not in every detail, with that of

Seward's *Rachiopteris Williamsoni*, which appears to be the petiole of some other species of *Sutcliffia*.

The vascular system of *Sutcliffia* has no parallel among any plants at present known, though a remote analogy may be traced with the anomalous structure of certain lianes belonging to the Sapindaceae. The genus is referred to the Medulloseae on account of the general organisation of the leaf-base and petiole, the numerous leaf-trace bundles, the tendency to dialystely shown in the formation of the subsidiary steles, and the histology of the vascular and cortical tissues.

The stem, however, has not deviated far from the monostelic condition, for the single central cylinder forms the dominant feature of the vascular system, while the meristeles serve to effect the transition to the leaf-traces. The plant is of considerable interest, as indicating the probable derivation of the Medullosean stem from a simple protostelic type, such as exists in *Heterangium* among the Lyginodendreae.

Fructification of Medulloseae.—There is one case in which we have clear and direct proof that a member of the Medulloseae, or, as we should rather say, of the Neuropterideae, was a seed-bearing plant. In the same year in which the seed of *Lyginodendron* was first identified, Mr. Kidston was able to demonstrate the presence of seeds in a species of *Neuropteris*, one of the genera which Stur, twenty years before, had proposed to exclude from the Ferns.

In the well-known species *N. heterophylla*, the frond of which is illustrated in Fig. 161 (p. 426), bodies of about the size of a hazel-nut, but relatively longer, were

discovered by Mr. Kidston, in nodules from the Middle Coal-measures of Dudley, attached to a rachis bearing the characteristic pinnules of *Neuropteris heterophylla*[1] (Fig. 169). The specimens are casts, not petrifactions, so no detailed study of structure has been possible, but the external characters leave no doubt that the organs in question are seeds. They are of the radially symmetrical type, and the testa has a fibrous structure. Chiefly on account of the latter character Mr. Kidston refers the seeds to the genus *Rhabdocarpus* of Göppert and Berger.[2] The seeds appear to be borne terminally on the fertile branches of the rachis; it is a striking fact that the seed-bearing frond or pinna should be so little modified as to show the same form of pinnule as the vegetative foliage; the differentiation of the

FIG. 169.—*Neuropteris heterophylla*. Seed, attached to a branch of the rachis bearing two characteristic pinnules. × 2. After Kidston.

[1] R. Kidston, "The Fructification of *Neuropteris heterophylla*," *Phil. Trans. Royal Soc.*, B, vol. cxcvii. 1904.

[2] Brongniart, however, limited the genus *Rhabdocarpus* to seeds with bilateral symmetry (Platyspermeae of Oliver), see Fig. 185, p. 513.

sporophyll had scarcely even begun in a case like this.

Mr. Kidston was thus the first to observe direct continuity between the seed and the frond in a Fern-like Palæozoic plant, and it was his discovery, in conjunction with the equally strong though less direct evidence in the case of *Lyginodendron*, which first suggested the institution of the class Pteridospermeae.

There is at present no instance of a petrified seed, showing structure, which can be referred to the Medulloseae or Neuropterideae with the same certainty as Mr. Kidston's casts. One of the best-known Palæozoic seeds, however, *Trigonocarpus Parkinsoni*, Brongn., may be attributed with great probability, as we shall see, to *Alethopteris*; we will therefore shortly describe its structure.

Trigonocarpus Parkinsoni is found in three distinct states of preservation in the English Coal-measures: (1) in the common condition of nut-like, somewhat triangular casts, which, as shown by Hooker and Binney and by Williamson, are really internal casts of the seed cavity; (2) as external casts, showing the testa and the true form of the seed; (3) as petrifactions, in which the structure is more or less perfectly preserved. From these various data a fairly complete knowledge of the organisation of the seed has been gained; its more important features are shown in the diagrammatic figures 170-172.

The seed is a very large one, the length reaching 5 cm., of which quite half is accounted for by the enormously long micropyle; the body of the seed has a maximum diameter of over 2 cm. (Fig. 170). The testa

consists of two clearly distinct layers—the outer layer or sarcotesta, composed of delicate, partly lacunar tissue, bounded externally by a sharply differentiated hypoderma and epidermis, and the inner ribbed sclerotesta, constructed, like the stone of a peach, of dense, thick-walled tissue. The ribs show a very definite arrangement. There are three principal ridges, corresponding to sutures, in the sclerotesta, and usually three secondary ridges in each space between the former, making twelve ribs in all (Fig. 171); within the sclerotesta there are some traces of an inner soft layer. The nucellus has a definite epidermis, and appears to have been free from the integument, from the chalaza upwards; it terminates at the apex in a dome-shaped pollen-chamber, provided with a long, narrow beak (Fig. 170, *p.c*, *p.c.b*), as in the seeds of the Cordaiteae, described in Chap. XII. The membrane of the megaspore or embryo-sac is evident, but the prothallus has not yet been found preserved.

The vascular system of the seed is double. At the base six bundles branch off from the common supply-strand and pass upwards through the sarcotesta (Fig. 170), taking a definite position opposite certain of the secondary ridges (Fig. 171). These bundles appear to have been collateral, with external phloëm, and there is evidence that the xylem was mesarch. The inner vascular zone formed a complex tracheal network in the nucellus; near the chalaza the sheath of nucellar tracheides is continuous; farther up they range themselves in longitudinal strands connected by abundant transverse anastomoses. The most remarkable feature of the seed is the long micropylar tube, formed by an extension of the ribbed sclerotesta, and enclosed in a

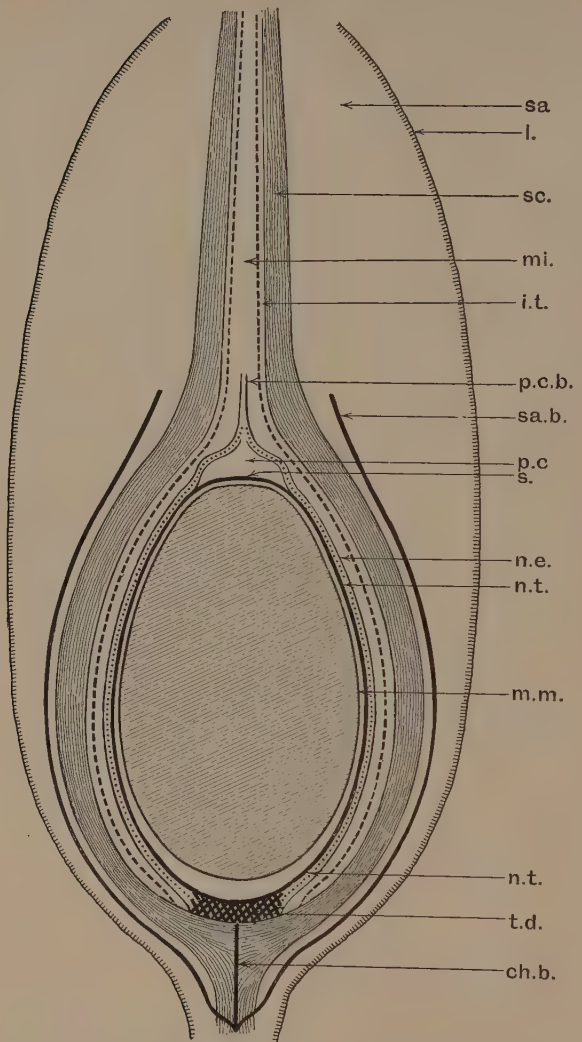

FIG. 170.—*Trigonocarpus Parkinsoni*. Diagrammatic median section in the plane of the "wing" (Fig. 172). *sa*, *sarcotesta*; *l*, its limiting layers; *sc*, sclerotesta; *mi*, micropyle; *i.t*, remains of "inner flesh"; *sa.b*, sarcotestal bundles; *p.c*, pollen-chamber; *p.c.b*, its beak; *s*, septum at bottom of pollen-chamber; *n.e*, nucellar epidermis; *n.t*, nucellar tracheal system; *m.m*, membrane of megaspore; *t.d*, tracheal disc at chalaza; *ch.b*, chalazal bundle. × about 3. From a drawing by Mr. A. J. Maslen, F.L.S.

broad, wing-like prolongation of the sarcotesta (Figs.

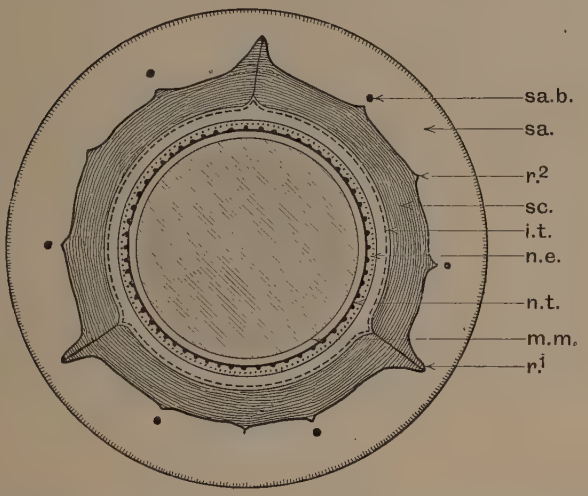

Fig. 171.—Diagrammatic transverse section through the body of the seed, at about the level of the line *m.m.* in Fig. 170; r^1, principal ridges; r^2, secondary ridges. Other lettering as in Fig. 170. × about 3. From a drawing by Mr. A. J. Maslen.

170, 172). It is not quite certain, however, to what

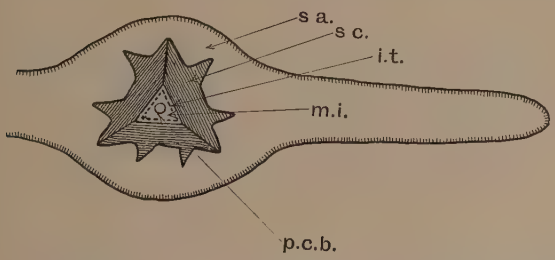

Fig. 172.—Diagrammatic transverse section through the micropyle, at about the level of the line *p.c.b.* in Fig. 170, showing the wing on one side. Lettering as in Fig. 170. From a drawing by Mr. A. J. Maslen.

extent the flattened form of this part of the seed is natural.

The seed, with its fleshy and stony coats, double vascular system, and pollen-chamber, is evidently very nearly akin to the seed of a recent Cycad, the chief difference consisting in the free nucellus, whereas in the modern family it is adherent to the integument.

The petrified specimens of *Trigonocarpus Parkinsoni* are, almost without exception, associated with the leaflets, petioles, and other organs of *Medullosa anglica*, while the casts very generally occur together with the *Alethopteris* foliage, which no doubt belonged to that plant and allied species of *Medullosa*. Histologically there is a striking agreement in the tracheides, a peculiar, finely scalariform type being characteristic both of the *Medullosa* and the *Trigonocarpus*. There is also a certain similarity between the limiting layers of the sarcotesta and those of the petiole. The evidence is of course far from amounting to proof, but the presumption is entirely in favour of this seed being the fructification of the *Alethopteris* (probably *A. lonchitica*), which formed the foliage of *Medullosa anglica*.[1]

No pollen-grains have yet been observed in the pollen-chamber of *Trigonocarpus*, but in another genus of the same group, *Stephanospermum*, Brongn., recently reinvestigated by Professor F. W. Oliver, they have been found in perfect preservation. The species to which Figs. 173 and 174 refer, *Stephanospermum akenioides*, Brongn., is one of the numerous seeds,

[1] On *Trigonocarpus* see Hooker and Binney, "On the Structure of certain Limestone Nodules enclosed in seams of bituminous Coal, with a description of some Trigonocarpons contained in them," *Phil. Trans. Royal Soc.* vol. cxlv. 1855. Williamson, "On the Organisation of the Fossil Plants of the Coal-measures," Part viii. *ibid.* vol. clxvii. 1877. Scott and Maslen, "The Structure of *Trigonocarpus*," *Ann. of Bot.* vol. xxi. 1907.

originally described by Brongniart, from the Black Pebbles of St. Croix, near St. Étienne, of Upper Coal-measure age. It is a comparatively small seed (measuring about 10 × 4.5 mm.), and, though the sarcotesta is not preserved, is evidently of the same general type as *Trigonocarpus*, with which it agrees in the radial symmetry, the prolonged micropyle, the beaked pollen-chamber, and the apparently free nucellus, of which the characteristic tracheal investment forms part.

The most striking peculiarities of the seed consist in the presence of a prominent ring or collar of the sclerotesta around the micropylar region, and in the nature of the nucellar tracheal system, which forms a continuous mantle of spiral or scalariform tracheides, extending as far as the pollen-chamber and spreading over its floor.

In this seed the prothallus is sometimes well preserved; the archegonia appear to have been only two in number; in the egg-cell the nucleus has been recognised.

The apex of the pollen-chamber was prolonged into a long beak or tube, engaging with the micropyle (cf. Fig. 170, *Trigonocarpus*).[1] Through this beak the pollen-grains entered the pollen-chamber, in which they are found in almost every seed. They also occur loose in the matrix, where they are of small size, averaging only about 60 μ in length, while the average dimensions of those in the pollen-chamber are 160 × 100 μ (210 μ being the extreme length observed), so that, as Renault first showed, the pollen-grains developed actively after

[1] In Fig. 173 the conical mass at the top of the figure represents the funnel-shaped base of the tube, but the tube itself is missed.

entering the seed. The multicellular structure of the pollen-grains, in this and other cases, was first demonstrated by Renault, and fully confirmed by the more recent observations of Oliver, who finds that there are about twenty cells in each grain, so arranged that five radial septa are seen when the grain is cut transversely

FIG. 173.—*Stephanospermum akenioides*. Upper part of pollen-chamber, showing part of its wall, with the base of the beak. In the chamber a large multicellular pollen-grain is shown, also three small foreign pollen-grains, one of which partly overlies the large grain. × 90. Will. Coll. 1486*a*. From a photograph lent by Prof. F. W. Oliver, F.R.S.

(Fig. 174). Ultimately the internal cells appear to have become retracted towards the periphery, leaving behind them in the middle of the grain a framework of cell-wall—the "replum" (see Fig. 174).

In the light of our present knowledge of the reproduction of *Ginkgo* and the Cycads it is an obvious suggestion that the internal cells of the pollen-grain were antheridial cells, producing spermatozoids.

Renault, however, actually anticipated the discovery of Ikeno and Hirase. In an allied seed, *Aetheotesta*, as well as in *Stephanospermum* itself, the cell-walls of the pollen-grains which they contain are perforated, and Renault suggested, in 1887, "that the perforations served for the passage of mobile bodies analogous to antherozoids." He adds: "We do not regard as

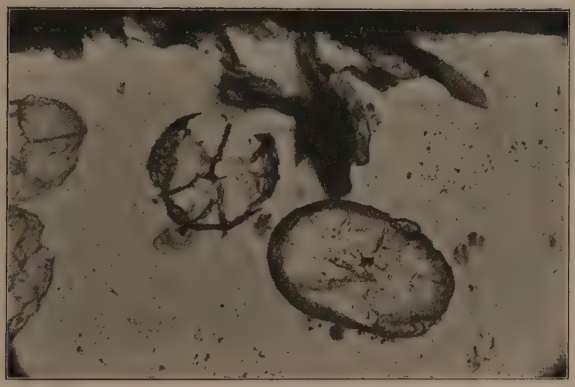

FIG. 174.—*Stephanospermum akenioides.* Multicellular pollen-grains in pollen-chamber; some shreds of the wall extend into the cavity. The middle pollen-grain is in transverse section, and shows the radiating septa dividing up the grain. The grain to the right is in longitudinal section, and shows the peripheral cells and the "replum" in the middle (see text). × 137. Univ. College Coll. S 7A. From a photograph lent by Prof. Oliver.

impossible the existence in the past of pollen-grains, which, instead of effecting fertilisation by means of a tube, discharged into the pollen-chamber of the appropriate seeds antherozoids capable of performing this function." [1]

[1] Renault, "Note sur le Genre *Aetheotesta*," *Mém. de Soc. d'Hist. Nat. de Saône-et-Loire*, pp. 156, 158, 1887. For *Stephanospermum* see Brongniart, *Graines Fossiles Silicifiées*, 1881; Renault, *Cours de bot. fossile*, t. iv. p. 184, Plates xxi. and xxii. 1885; F. W. Oliver, "Structure and Affinities of *Stephanospermum*," *Trans. Linn. Soc. London*, 2nd ser. Bot. vol. vi. Part viii. 1904.

Renault's prescience has been fully justified by subsequent discoveries; possibly even the direct proof of the existence of spermatozoids in fossil Seed-plants may yet be obtained.[1]

The presence of a pollen-tube in the case of *Stephanospermum* and other Palæozoic Spermophytes is very doubtful. Small papillae are occasionally observed (as in the large pollen-grain shown in Fig. 173), but their significance is still uncertain. Some further reference to the question will be made in discussing the fertilisation of the Cordaiteae (Chap. XII. p. 543).

It is only in the case of *Neuropteris heterophylla* that we have, as yet, the direct proof that Neuropterideae bore seeds; as we have seen there is strong, though less conclusive, evidence that the seed *Trigonocarpus Parkinsoni* belonged to *Medullosa anglica*, which, according to its foliage, was certainly an *Alethopteris*.

A considerable mass of evidence, mainly from association, has further been accumulated through the extensive investigations of M. Grand'Eury both in the Upper Coal-measures of Central France and in the more ancient deposits of Belgium, Northern France, and the Saar Valley. This observer, whose experience in such researches is unrivalled, finds that the vegetative organs of Neuropterideae, wherever there is evidence that they grew *in situ*, are constantly associated with seeds of the radially symmetrical type, such as rarely occur in company with plants of any other group; he further finds special types of seed in close association with

[1] Evidence on this subject is adduced in Prof. F. W. Oliver's memoir "On *Physostoma elegans*," *Ann. of Bot.*, January 1909.

definite genera and species of frond. Considering the wide field covered by M. Grand'Eury's observations, and the fact, which he established, of the social growth of plants of the same group, there can be no doubt of the value of the conclusions arrived at. M. Grand'Eury is led to refer some fifteen genera or sub-genera of seeds to the Neuropterideae, the general characters of the seeds being that they are of radial symmetry, and striated, polygonal, or winged, the number of the angles or wings being some multiple of three.

Among Grand'Eury's special results we may mention that he refers the huge seed *Pachytesta gigantea* (sometimes 4 inches long) to a species of *Alethopteris* (*A. Grandini*) and smaller seeds of the same type to other species of the genus. In the Northern Coal-fields, however, he finds *Trigonocarpus* seeds associated with certain Alethopterids (in agreement with our conclusion as to *T. Parkinsoni*), and points out the affinity between *Pachytesta* and *Trigonocarpus*.

A considerable variety of seeds is referred to *Neuropteris*; the seed attributed to *N. flexuosa* appears to be of the same type as that of *N. heterophylla*, discovered by Kidston.

Various seeds are also referred (not to mention other cases) to the genera *Odontopteris* and *Linopteris* (= Dictyopteris), which are some of those which Stur had already removed from the Ferns in 1883.

M. Grand'Eury has in several cases detected the "inflorescence" or fertile rachis on which the seeds were borne, but details have not yet been published. He is of the opinion that, as a rule, the organs of reproduction of Neuropterideae and other Pteridosperms

were borne "on special organs, separate from the leaves, *i.e.* on independent inflorescences." In *Neuropteris heterophylla*, however, and in other cases, to be subsequently mentioned, the seeds were borne on a frond but slightly modified, so there can be little doubt that the organ supporting them, even when more specialised, was still foliar in nature.[1]

We have as yet very little knowledge as to the nature of the male organs in the Neuropterideae. In 1887 Mr. Kidston described a form of fructification in *Neuropteris heterophylla*, the species in which he subsequently discovered the seed. The specimen[2] consists of a forked rachis, bearing the normal vegetative pinnules below, while the branches terminate in four-lobed bodies, which may be interpreted either as groups of sporangia or as cupules. As there is no evidence for the presence of cupules of this kind in Neuropterideae, the former interpretation is somewhat the more probable, in which case the specimen would no doubt represent the microsporangiate fructification. M. Grand'Eury has also observed a rachis bearing sporangium-like bodies in *Neuropteris*, and "floral discs," which he regards as male, in *Linopteris*, but our information is still too imperfect to allow of the subject being pursued further at present.

M. Grand'Eury has recently found evidence that

[1] C. Grand'Eury, "Sur les Graines des Neuroptéridées," *Comptes Rendus*, t. 139, pp. 23 and 782, 1904; "Sur les Inflorescences des Fougères à Graines du Culm et du Terrain Houiller," *Comptes Rendus*, t. 143, p. 761, 1906.

[2] The figure and description are reproduced in Mr. Kidston's paper on "The Fructification of *Neuropteris heterophylla*," above cited.

various Neuropterideae possessed stolons and other means of vegetative propagation.[1]

Affinities of Medulloseae

We may provisionally treat the family names Medulloseae and Neuropterideae as synonymous, for though there can as yet be no strict proof that the groups indicated were coextensive, yet there is evidence that the Medullosean type of structure existed in several of the genera with Neuropteridean characters in the frond.

In the Medulloseae, as in the Lyginodendreae, we are able to point to definite structural characters, quite apart from the habit, which indicate affinity with the Ferns. So far as *Medullosa* itself is concerned, the most Fern-like feature is the vascular system of the stem, which in its primary "polystelic" arrangement appears essentially Filicinean, and was compared by Weber and Sterzel in 1896 with that of *Psaronius*. The fact that this original ground-plan becomes more or less obscured as secondary growth goes on does not affect the significance of the primary structure, but a more serious difference from the Ferns consists in the absence of leaf-gaps in *Medullosa* (see above, p. 444). The discovery of the *Sutcliffia* type of vascular system, which may be described as a modified protostele, renders it probable that polystely arose within the family Medulloseae, and if so we must regard this character rather as a parallel development to the polystely of the Ferns than as a direct inheritance from them. In

[1] C. Grand'Eury, "Sur les organes et le mode de végétation des Neuroptéridées, et autres Ptéridospermes," *Comptes Rendus*, t. 146, p. 1241, 1908.

Sutcliffia, however, the anatomy of the stem, peculiar as it is, can only be compared with that of a protostelic Fern, while the concentric foliar bundles accentuate the relationship. There is nothing as yet to indicate from what group of primitive Ferns the Medulloseae may have sprung, and indeed the great complexity of the seed shows clearly enough how remote the Fern-connection must have been. On anatomical grounds it seems not unlikely that this family may have had a common origin with the Lyginodendreae from some unknown protostelic type.

On the whole, the Medulloseae or Neuropterideae strike one as a more advanced group than the Lyginodendreae. Their seeds, if we may take *Trigonocarpus* as a type, perhaps approach nearer than any other Palæozoic seeds to those of recent Cycadaceae, as shown by the differentiation of the integument into a sarcotesta and a sclerotesta, the double vascular system and the form of the pollen-chamber; the chief difference lies in the apparently free nucellus of the fossil seeds, a feature with which other distinctions may be correlated. As regards anatomical characters, the petiole and rachis of *Medullosa* very closely resemble those of a Cycad in structure; the same may be said of the root. The stem-structure, however, throughout the Medulloseae is essentially different, for neither in the almost protostelic *Sutcliffia*, nor in the more complex polystelic stems of *Medullosa*, do we find, as it seems to me, any fundamental agreement with the stem either of recent Cycadaceae or of Mesozoic Bennettiteae, though certain analogies can be traced. On the whole of the evidence an affinity between the Medulloseae and the Cycado-

phyta of later periods appears well established, but we cannot for a moment suppose that the former were the direct ancestors of the latter. The question will receive some further consideration in the final chapter.

ANEIMITEAE

The genus *Aneimites*,[1] Dawson, may be mentioned in connection with the Neuropterideae, to which it has sometimes been referred on foliar characters, though, as we shall see, the fructification shows that there can have been no near affinity. The habit of the fronds is like that of a Maiden-hair Fern (*Adiantum*), as the original generic name *Adiantites* implied; the genus extends from the Devonian to the Middle Coal-measures, and is characteristic of the Lower Carboniferous. In a species (*Aneimites*[2] *fertilis*) from the Pottsville beds of West Virginia, of an age corresponding to that of our Millstone Grit, Dr. David White has demonstrated the presence of seeds on the fronds. They are borne on the apices of branched, terminal extensions of the peripheral pinnae; the pinnules on the adjacent sterile portions of the frond, though considerably reduced, retain the characteristic cuneiform shape. The small seeds (averaging 4.5 mm. in length) are rhomboidal in form, lenticular in cross-section, and winged; it thus appears that they were of the platyspermic (bilaterally symmetrical) type, which was once supposed to characterise the Cordaiteae. As the specimens are only

[1] David White, "The Seeds of *Aneimites*," *Smithsonian Miscellaneous Collection*, vol. xxvii. p. 322, 1904.

[2] It is to be regretted that the older and more familiar name, *Adiantites*, Göppert, has had to be abandoned, on grounds which will only appeal to the specialist in nomenclature.

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known in a carbonised condition, nothing certain can be said as to the structure, though the discoverer believed that he detected indications of the micropyle and pollen-chamber. The isolated seeds were named *Wardia fertilis* before their connection with the frond was observed. Dr. White has discovered different forms of the *Wardia* seeds in the most intimate association with four other species of the genus; in one of these, *A. tenuifolius*, Göppert, they again occur in actual connection with the frond. The author points out that the proof of the Pteridospermous nature of *Aneimites* throws suspicion on various similar frond-genera, in one of which, *Eremopteris*, there appears to be strong evidence from other sources for the occurrence of seeds of a platyspermic type. The seeds of *Aneimites* resemble some of those grouped under the name *Cardiocarpon*, and it may be hoped that this clue may eventually lead to the recognition of their structure.

Seed-bearing Pecopterideae

Up to the year 1905 the form-genus *Pecopteris* was regarded as the stronghold of the true Ferns, no suspicion of other alliances attaching to any of its members. In that year, however, M. Grand'Eury made the striking discovery that the species *Pecopteris Pluckeneti*, from the Upper Coal-measures of St. Étienne, was a seed-bearing plant.[1] In twenty specimens he found the seeds attached by hundreds to the fronds. Sometimes they occur on pinnae of the usual vegetative form, but where they are numerous the lamina is somewhat reduced. The seeds

[1] "Sur les Graines trouvées attachées au *Pecopteris Pluckeneti*, Schlot.," *Comptes Rendus*, t. cxl. p. 920, 1905.

are attached at the ends of the stout lateral veins of the pinnules (see Fig. 175). They are described as forming a wide angle, when in the natural condition, with the plane of the lamina, so that they no doubt hung down freely from the under side of the fertile frond. The seeds, like those of *Aneimites*, are winged (Fig. 175), and resemble *Samaropsis*, the seed of the Gymnosperm *Dorycordaites* (see p. 520) so closely, that the two may easily be confused when found isolated.

The species *P. Pluckeneti* belongs to a section of the genus characterised, according to Professor Zeiller, by the large, lobed pinnules, and the dichotomously branched frond, with a bud, capable of further growth, in the axil of each bifurcation.[1] Though usually included in *Pecopteris*, some authors have placed the species in other genera, and notably Sterzel, in 1883, founded a new genus, *Dicksoniites*, for its reception, because he observed, in some specimens, round discs at the margins of the pinnules, which he compared to the sori of *Dicksonia*.[2] The nature of these bodies appears to have been elucidated by a recent observation of M. Grand'Eury's. He states that he found "stellate groups of anthers in the place of the receptacles," and that they were borne on different specimens from those

FIG. 175.—*Pecopteris Pluckeneti*. Fragment of a fertile pinna with seeds attached near the ends of the lobes. ×3. From Zeiller, after one of Grand'Eury's specimens.

[1] Zeiller, *Éléments de Paléobotanique*, p. 89, 1900.

[2] "Über *Dicksoniites Pluckeneti*," *Bot. Centralblatt.* Bd. xiii. 1883.

showing seeds. We may hope for more detailed information on this interesting point.[1]

There is another species of *Pecopteris*, *P. Sterzeli*, Zeiller, which so closely resembles *P. Pluckeneti*, in the form and mode of branching of the frond, that Professor Zeiller has no doubt that this too was a Pteridosperm, though the seeds have not yet been observed. There is evidence of considerable weight that the fronds of *P. Sterzeli* were borne on a *Caulopteris* stem—*Caulopteris*, as already stated, representing the casts of "Tree-fern" stems, the structure which, when known, is that of *Psaronius* (Vol. I. p. 295). Although Professor Zeiller no longer regards the connection between *Pecopteris Sterzeli* and the *Caulopteris* as proved, it seems desirable to call attention to the question, for there appears to be little reason for doubting the evidence, beyond the *à priori* improbability of a seed-bearing plant having had the stem of a supposed Marattiaceous Tree-fern.[2] If Professor Zeiller's original opinion should be confirmed by future investigation, the relation of the Marattiaceous to the Pteridospermous Pecopterids will need serious reconsideration.

It has already been mentioned (Vol. I. p. 289) that additional evidence for the Pteridospermous nature of certain Pecopterids is afforded by the fact that they bore fructifications of the *Crossotheca* type. Mr. Kidston[3] enumerates three species of *Crossotheca* in which the foliage is known to have been that of a

[1] See Grand'Eury, "Sur les Inflorescences des Fougères a Graines," etc., *Comptes Rendus*, t. cxliii. p. 764, 1906.

[2] For the history of this question *see* Zeiller, *Flore Fossile de Commentry*, Pt. i. t. 1888, p. 184, Plate viii.; *Bassin Houiller et Permien de Blanzy*, *Flore Fossile*, 1906, p. 62.

[3] *Microsporangia of the Pteridospermeae*, p. 432.

Pecopteris, and there are two other species in which this was probably the case. As Mr. Kidston says: "Having shown that the supposed sporangia of one species of the genus [*Crossotheca*] are in reality the microsporangia of one of the Pteridosperms, I think we are justified in provisionally concluding that all the remaining species also belong to the Pteridospermeae, even though we do not possess a complete knowledge of the structure of their microsporangia." There is thus a presumption that a considerable fraction of the old genus *Pecopteris* is made up of seed-bearing plants.

One of the probable Pecopteroid Crossothecas, *Pecopteris exigua*, Ren.,[1] from the Permo-Carboniferous of Autun, occurs in the silicified condition, with structure preserved, but only fertile portions of the frond appear to be known. The little fertile pinnules, elliptical in form and about 1 mm. long, are inserted on the rachis like the leaflets of a *Pecopteris*. Each pinnule bears, on its lower surface, two rows of ovoid, pointed sporangia, three or four in each row; they appear to be free from each other, and do not show the bilocular structure described by Mr. Kidston in the *Crossotheca* of *Lyginodendron*. There is, of course, no proof that they were microsporangia, but the general resemblance to a *Crossotheca* tells in favour of this supposition.

In *Callipteris*, a characteristic Permian genus of comparatively small bipinnate fronds, placed by M. Zeiller in Pecopterideae, M. Grand'Eury has found evidence that seeds were present in at least two species. The seeds, which appear to have been borne on a slender,

[1] Renault, *Cours de Bot. Fossile*, année 3, p. 115, Plate xix. Figs. 13-18, 1883.

branched rachis, are of an elliptical or roundish shape, and from 5 to 10 mm. in length, and are described as resembling berries, and as the simplest in form of any Pteridospermous seeds. Bodies resembling an enormous *Crossotheca*, 2 to 3 cm. in length, and bearing marginal sporangia, are regarded as possibly constituting the male organs of the plant. M. Grand'Eury points out that *Callipteris* differs widely from the Neuropterideae in its organs of reproduction as well as in foliar characters.[1]

The common Coal-measure "Fern," *Mariopteris muricata*, with forked primary pinnae and a *Lygodium*-like habit, has quite recently been found by M. Grand'Eury in close association, if not in connection, with small seeds,[2] so it is probable that this Pecopteroid form, in which no Fern-like fructification has ever been observed, will likewise prove to belong to the Pteridosperms.

We see then that on present evidence there is every reason to believe that a large proportion of the Fern-like Palæozoic plants with Pecopteroid foliage will find their place, like *Pecopteris Pluckeneti*, among seed-bearing plants. As we have already seen (Chap. VIII. Vol. I.) there are still good grounds for the opinion that some other Pecopterids were true Ferns; much further investigation will be necessary before we are able to discriminate with certainty between the two classes of plants represented among fossils of this habit.

[1] Grand'Eury, "Sur les Graines et Inflorescences des *Callipteris*," *Comptes Rendus*, t. cxliii. p. 664, 1906.

[2] Grand'Eury, "Sur les organes et le mode de végétation des Neuroptéridées et autres Ptéridospermes," *Comptes Rendus*, t. cxlvi. p. 1243, 1908.

Summary on the Pteridosperms

We have now completed our sketch of those Fern-like Palæozoic plants in which there is reason to believe that seeds were produced. Direct and conclusive evidence is still limited to a few instances, but these few are widely distributed. The fully established cases of *Lyginodendron oldhamium*, *Neuropteris heterophylla*, *Aneimites fertilis*, and *Pecopteris Pluckeneti* represent four distinct families,[1] in each of which there is further a considerable body of collateral evidence, varying in its degree of cogency, but all pointing the same way, so as to leave no doubt that the seed-bearing habit was very widely spread. Fragmentary as our knowledge at present is, it is sufficient to establish a strong probability that a large majority of the Fern-like plants of Palæozoic age were Spermophytes.

It is obvious that it would be altogether premature, in the present rudimentary state of our knowledge, to attempt to define the limits of the Pteridospermeae or to assign them precise characters. As regards the extent of the Class, it no doubt embraced most of the Neuropterideae and Sphenopterideae, a considerable part of the Pecopterideae, and various outlying genera, such as *Aneimites* and *Eremopteris*. It is impossible to tell how much further the limits of the group may be extended by further research. Equal caution is necessary in attempting to draw up the characters of the Pteridospermeae, for it is only in comparatively

[1] *Aneimites* (*Adiantites*) was placed by Professor Zeiller, on account of its frond-characters, in the Neuropterideae; the form of the seeds, however, indicates that the affinities of the genus lie in a different direction.

few cases that we have any knowledge of structure. Provisionally, the following diagnosis, agreeing with that already given in Chapter X. (p. 356), may serve the purpose of distinguishing the group from the other Palæozoic seed-plants.

> Male and female sporophylls little differentiated from the vegetative foliage; no cones formed. Anatomy of either stem or leaf or both, of a Filicinean type, as was also the habit.

The first part of this diagnosis requires a word of explanation, as it appears inconsistent with M. Grand'Eury's opinion that the reproductive organs were usually borne on special inflorescences. The part of the sporophyll immediately bearing the seeds or microsporangia may be modified by suppression or alteration of the lamina, but in many cases (*Neuropteris*, *Aneimites*, *Pecopteris Pluckeneti*, *Crossotheca*) the fertile rachis forms part of an otherwise normal foliage-leaf, and this may have been so generally. Even where no pinnules have been found in connection with the fertile rachis, the latter resembles that of the vegetative leaf in its branching. We may safely take it as a character of the Pteridosperms that their sporophylls were more like the foliage-leaves than in any other group of Spermophyta; in some cases they are even less modified than in many Ferns.

No diagnostic character can at present be based on the seed itself; the radially symmetrical seeds of *Lagenostoma* and *Trigonocarpus* are no doubt characteristic of certain families of Pteridosperms, but nothing is known of the structure of the platyspermic type of seed found in *Aneimites* and *Pecopteris Pluckeneti*;

these seeds cannot, therefore, be distinguished from those of the Cordaiteae, to be considered in the next chapter. The presence of a pollen-chamber and of a well-developed vascular system are characters which the seeds of the Pteridosperms share with those of the Cordaiteae, Cycadaceae, and Ginkgoaceae.

As regards the male organs our information is too limited to allow of any generalisation; so far as appears at present the microsporangia of the Pteridosperms did not differ essentially from the isosporangia of Marattiaceous Ferns.

The anatomical characters have already been discussed at some length, and further reference will be made to them in the concluding chapter. There is probably no constant distinctive character in the structure of either stem or leaf; but taking the *sum* of the anatomical characters the Pteridosperms, so far as we know, appear to have retained much more of a Fern-like organisation than any of the true Gymnosperms. As we have already seen, it is probable that both Medulloseae and Lyginodendreae were derived from some simple protostelic Fern-type, *Sutcliffia* on the one hand and *Heterangium* on the other showing a convergence in that direction.

Other Cycadofilices

There are a certain number of fossil plants which cannot yet be classed as Pteridosperms because we have no evidence as to their fructification, but which, from their vegetative characters, appear to belong to the same great class of plants. For such fossils, Potonié's

name Cycadofilices may be provisionally retained. Some of these very varied forms will now be shortly described.

Megaloxyleae

Professor Seward some years ago described the structure of an interesting stem from the Lower Coal-measures of Lancashire, which he made the type of a new genus of Cycadofilices, under the name of *Megaloxylon Scotti*.[1] The specimen, which consists of the wood only, is between 4 and 5 cm. in diameter, the central primary wood having a maximum diameter of nearly 2 cm., while the rest is made up of the secondary xylem-zone. The structure bears a general resemblance to that of *Heterangium*, but differs from the latter genus in several important points. The stem has no pith; the whole central region of the stele is occupied by the primary wood, which has a very remarkable structure. The greater part, which may be termed the metaxylem, consists of large, usually very short tracheides, often broader than long, interspersed with tracts of thin-walled parenchyma. This tissue is interrupted by large horizontal gaps, probably due to shrinkage, and recalling the appearance of the discoid pith of *Cordaites*.[2]

Five large leaf-trace strands are ranged round the periphery of the primary wood. Their arrangement points to a $\frac{2}{5}$ phyllotaxis. Each trace is made up of elongated pitted tracheides, separated by vertical rows of short parenchymatous cells. At the extreme out-

[1] A. C. Seward, "Notes on the Binney Collection of Coal-measure Plants," Part ii. *Megaloxylon*, *Proc. Cambridge Phil. Soc.* vol. x. 1899, p. 158.

[2] Similar gaps occur in the pith of *Pitys antiqua*. See below, p. 515.

side of the trace, adjacent to the secondary wood, are several groups of spiral elements (protoxylem), showing that the xylem of the bundles of *Megaloxylon* was centripetally developed, or *exarch*, as distinguished from the mesarch strands of *Heterangium* or *Lyginodendron*.

As the leaf-trace is followed downwards into the stele, it is found to spread out laterally, in a fan-like form, its tracheides becoming shorter and more irregular, until they gradually become merged in the metaxylem. The leaf-trace passes through about four internodes, at the periphery of the primary wood, before losing its individuality.

The secondary wood requires little description. It is of the *Lyginodendron* type, and is characterised by the author as practically identical with that of *Cycadoxylon robustum*, described below (cf. Fig. 178, p. 483).

The large leaf-traces can be followed, as they pass obliquely outwards through the secondary wood, enclosed by a secondary zone of their own, continuous on the exterior with that of the stem itself. Professor Seward infers that the trace was probably concentric in structure.

The most essential points of difference from *Heterangium*, which are sufficient to place *Megaloxylon* provisionally in a distinct family, are, first, the exarch structure of the primary wood, and secondly, the peculiar form of the short tracheides of the metaxylem, which may probably have served for the storage rather than for the conduction of water.

The former character is shared by *Sutcliffia* among the Medulloseae, with which there is otherwise nothing to connect *Megaloxylon*. The short tracheides of the central

wood reappear in *Zalesskya diploxylon*, a Permian plant recently described by Kidston and Gwynne-Vaughan,[1] and shown by them to be a primitive member of the Osmundaceae. In the *Zalesskya*, however, there is no xylem-parenchyma, and many other differences forbid the suggestion of affinity. The conversion of the central wood into a water-reservoir, as it became superfluous for conducting purposes, may well have happened in more than one line of descent (cf. *Lepidodendron selaginoides*).

The position of the genus is best defined in the words of its discoverer :—

"*Megaloxylon* adds another connecting link between the Palæozoic Cycadofilices and recent Ferns; in anatomical characters the two genera *Lyginodendron* and *Heterangium* approach most nearly to the Osmundaceae and Gleicheniaceae respectively; in *Megaloxylon*, on the other hand, the structure of the primary xylem affords evidence that the *Lygodium* type of stem was also represented in the Cycad-Fern alliance which played so prominent a part in Palæozoic vegetation."[2]

A more complete knowledge of the plant will be necessary before its affinities can be determined.

Calamopityeae

Calamopitys.—While *Megaloxylon* recalls in a general way the structure of *Heterangium*, the plants next to be considered show a type of anatomy comparable to that of *Lyginodendron*, though here also the differences

[1] "On the Fossil Osmundaceae," Part ii. *Trans. Royal. Soc.* Edinburgh, vol. xlvi. Part ii. p. 226, 1908.

[2] Seward, *l.c.* p. 171.

appear to justify a separate family-name.[1] Several species, of Lower Carboniferous and Devonian age, are known, all of which are at present referred to the genus *Calamopitys* of Unger. The generic name is unfortunate, as it suggests an affinity with *Calamites*, with which, as all recent investigations have shown, the genus has nothing whatever to do, while the relationship to *Lyginodendron* is clear.

The species of which we have the most complete knowledge is *Calamopitys Saturni*, Unger, from Saalfeld in Central Germany; Count Solms-Laubach, to whom we owe a full account of its anatomy,[2] now regards the horizon as Devonian,[3] and not, as was previously believed, Lower Carboniferous.

Only three or four fragmentary specimens are known, the largest of which is about 1.5 cm. in diameter (see Fig. 176).

The stem has a small pith (1 to 2 mm. in diameter) surrounded by the primary wood, which consists of about half a dozen bundles, apparently somewhat confluent with each other laterally.[4] In the middle of each xylem-strand is a group of small elements, no doubt constituting the protoxylem. The primary strands of xylem abut more or less immediately on the surrounding zone of secondary wood, the elements of

[1] In this I now follow Count Solms-Laubach. In the previous edition *Calamopitys* was included under Lyginodendreae.

[2] "Pflanzenreste des Unterculm von Saalfeld." *Abhandl. der k. preuss. geol. Landesanstalt*, neue Folge, Heft 23, p. 63, 1896. A true Calamite, now known as *Arthrodendron*, was described by Williamson under the same name, *Calamopitys*; see Chapter II. p. 34.

[3] "Die Bedeutung der Paläophytologie für die systematische Botanik," *Mitt. der philomath. Gesellsch. in Elsass-Lothringen*, Bd. iii. 1906.

[4] A doubtfully distinct species, *C. annularis*, differs in the larger pith (7 mm.) and the more confluent xylem-strands.

which are radially arranged; the wedge-shaped groups of secondary tracheides are separated from one another by medullary rays, usually more than one cell in thickness. The sculpturing of the tracheides consists of several rows of crowded circular pits, limited to the

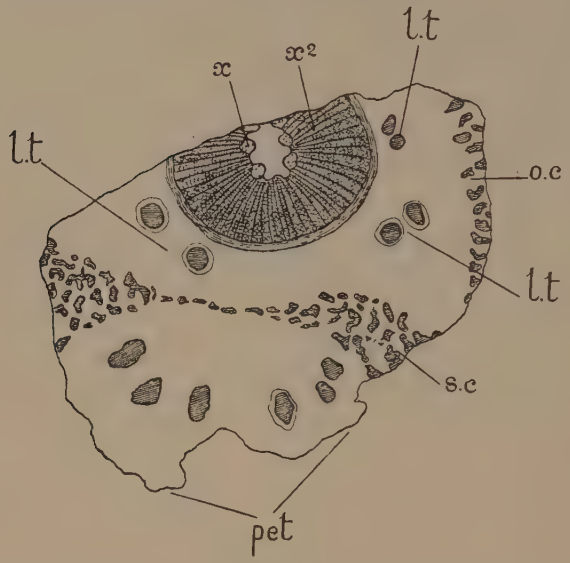

FIG. 176.—*Calamopitys Saturni*, Unger. Transverse section of stem. *x*, primary xylem-strands; x^2, secondary wood; *o.c*, outer cortex, with fibrous strands; *l.t*, double-leaf-traces; *pet*, petiole-base, containing six bundles; *s.c*, sclerenchyma at junction of petiole with stem. × about 4. After Solms-Laubach.

radial walls in the case of the secondary elements, but occurring on all sides of those tracheides which belong to the primary wood.

The phloëm is preserved in one fragment, and contains bast-fibres, in addition to the elements of the soft bast. The wide inner cortex is parenchymatous, while its outer zone is strengthened by strands of hypo-

dermal fibres, as in *Heterangium* and other genera (Fig. 176, *o.c*).

The cortex is traversed by the large leaf-trace bundles (*l.t*). The trace, when it first leaves the wood, is a single bundle, but immediately divides into two, precisely as in *Lyginodendron*. The leaves were spirally arranged, and the phyllotaxis appears to have followed the $\frac{2}{5}$ arrangement. Each transverse section constantly includes the trace-bundles of five successive leaves, which appear to have been more crowded than in *Lyginodendron*, for the same transverse section may show two leaf-bases in connection with the stem. The petioles were of large size, even exceeding the stem itself in diameter.

The characters shortly described, according to the investigations of Count Solms, to whom our whole knowledge of the anatomy of this species is due, agree so closely with those of *Lyginodendron*, that even a generic separation would scarcely seem justified, if it were not for two points which are still to be mentioned. One of these is the fact that the leaf-trace bundles appear to have assumed concentric structure immediately on entering the cortex of the stem ; the other and more important point is that, on entering the leaf-base, the two bundles underwent further divisions, so that the petiole contained half a dozen bundles or more, instead of two at most, as in *Lyginodendron*. The leaf-stalks, characterised by the ring of large vascular bundles and the hypodermal strands of sclerenchyma, would fall into the old genus *Kalymma*, one of the numerous fossil genera founded on isolated organs of plants, which subsequent research is gradually enabling us to identify.

The free *Kalymma* petioles contain many bundles and are known to have branched; there is little doubt that they represent the stalks of compound Fern-like leaves.

Their structure is so different from that of the petiole in Lyginodendreae that it is best to keep the families distinct, especially as we know nothing of the reproduction of Calamopityeae. I have recently identified specimens of *Calamopitys* in material from the Upper Devonian of Kentucky, sent me by Professor E. C. Jeffrey, and *Kalymma* has long been known from similar horizons. The great antiquity of the genus is thus well established.

Two other species may be shortly described. In *C. fascicularis*,[1] from the Lower Carboniferous of Dumbartonshire and the North of England, only the pith and wood are known, but their structure is well shown (see Fig. 177). The small pith (2 to 3 mm. in diameter) is surrounded by a circle of distinct primary xylem-strands, eight or nine in number. These strands are very unequal in size, attaining their maximum diameter where they leave the pith to pass outwards through the secondary wood (Fig. 177, B and A). Traced downwards from this point they diminish rapidly in size, and each strand unites with a small "reparatory" strand on the side corresponding to the downward (kathodic) direction of the leaf-spiral (see Fig. 177 and the description). The comparison of successive sections shows that the phyllotaxis was $\frac{2}{5}$ and that the course of the xylem-strands was essentially the same as in *Lyginodendron*. The strands can be followed out

[1] D. H. Scott, "On the Primary Structure of certain Palæozoic Stems with the *Dadoxylon* Type of Wood," *Trans. Roy. Soc.* Edinburgh, vol. xl. Part ii. 1902.

through the secondary wood, and evidently belonged to the leaf-trace bundles. Their structure is typically mesarch; in the large strands, approaching their exit,

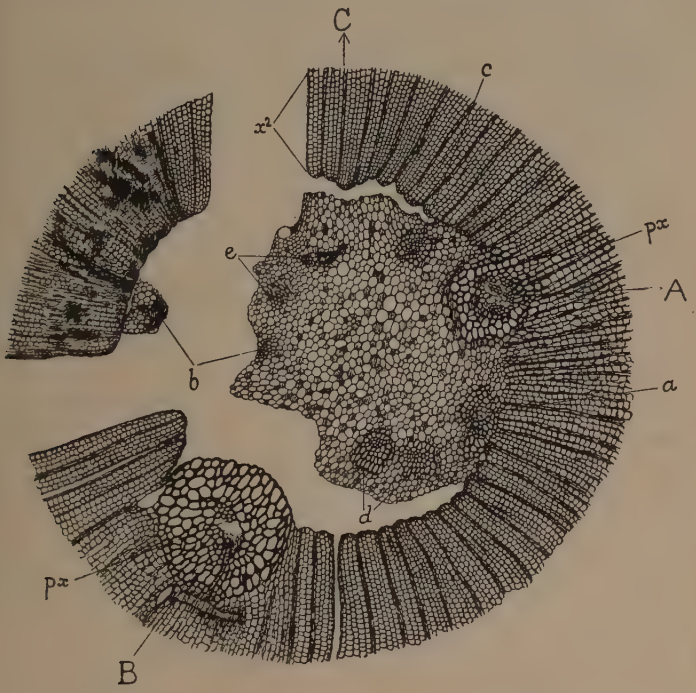

FIG. 177.—*Calamopitys fasciculariis*. Transverse section of central part of stem, showing the pith (rather contracted), the primary xylem-strands, and part of the secondary wood. A, large xylem-strand, about to pass out to a leaf; B, still larger strand, already on the way out; *px*, protoxylem-groups; C (arrow), direction of another outgoing strand; *a*, *b*, *c*, reparatory strands of the bundles A, B, C. *d*, *e*, main and reparatory strands of two other leaf-traces, lower down in their course. × 20. Kidston Coll. 540A. (G. T. G.)

the protoxylem is central; lower down, as the strand diminishes in diameter, the centripetal wood becomes relatively reduced in amount. In the lower part of their course the xylem-strands become embedded in

the pith (Fig. 177, *d* and *e*). The secondary wood has a dense structure, with narrow medullary rays, one or at most two cells thick, and resembles that of the Cordaiteae (see Chapter XII.). The tracheides bear multiseriate bordered pits. An interesting peculiarity is the presence of wide and short tracheides in the inner layers of the secondary wood; presumably they served, like the similar primary tracheides of *Megaloxylon* and *Zalesskya*, for water-storage, but here they form part of the secondary tissue-system.

Another species, *Calamopitys Beinertiana*,[1] occurring in the Calciferous Sandstones of the Tweed, and at Falkenberg, in Silesia (Lower Carboniferous or possibly Devonian) is remarkable for the large pith, containing "sclerotic nests" like those of *Lyginodendron*. The numerous primary xylem-strands resemble those of the last species, except in the interesting fact that in the lower part of their course they become endarch, losing their centripetal wood altogether—a first approach towards the structure of the typical Gymnosperms. In this species a scale-bark was formed on the older stems.

The Calamopityeae show clear affinity with *Lyginodendron* in the structure and arrangement of the primary strands of wood; in the secondary wood they approach nearer to the Cordaitean type; the structure of the petioles (not yet investigated in sufficient detail) is peculiar, and rather recalls Medulloseae than Lyginodendreae. The family evidently formed one branch of

[1] The *Araucarites Beinertianus* of Göppert. See Scott, *l.c.* p. 341.

the great plexus of Palæozoic forms lying on the confines of Ferns and Gymnosperms.

Cycadoxyleae

We have now to consider a series of fossil forms of which our knowledge is still imperfect, but which are of great interest, as they appear to connect the Lyginodendreae with a more distinctly Cycadean type of structure.

A portion of a large stem, *Cycadoxylon robustum*, regarded by Williamson as belonging to *Lyginodendron*, and subsequently named *L. robustum* by Professor Seward, was discovered by Nield more than thirty years ago, in the Lower Coal-measures of the Oldham district. Although the specimens are fragmentary, they show some points of considerable interest. No cortical tissues are preserved, and even the wood is probably incomplete, but the remaining, central part of the stem has a diameter of about 14 cm., so, in the natural condition, the plant must have reached the dimensions of a small tree. The secondary wood, which, in its present state, has a thickness of nearly 6 cm., resembles that of *Lyginodendron oldhamium* (Fig. 178, x^2). The medullary rays are broad, and of great height, so that the whole character of the wood was very parenchymatous, like that of the recent Cycads. The tracheides, which have a somewhat sinuous course, bear multiseriate bordered pits on their radial walls.

The pith, which is almost 3 cm. in diameter, is imperfectly preserved, but there are distinct remains of

scattered, dark groups of sclerotic tissue, such as we find in the pith of *L. oldhamium.*

The most characteristic feature of *Lyginodendron*, however, namely the strands of primary wood on the

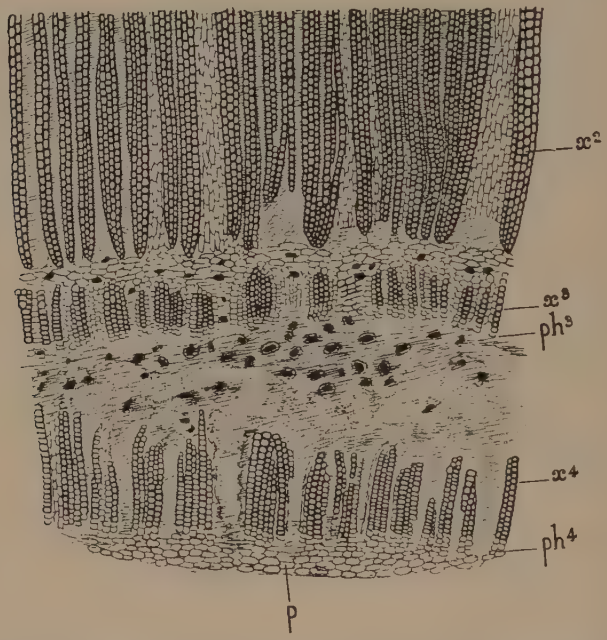

FIG. 178.—*Cycadoxylon robustum.* Part of transverse section, showing inner portion of normal wood, with two anomalous zones of wood and bast. x^2, normal secondary wood; x^3, ph^3, first inverted band of medullary xylem and phloëm; x^4, ph^4, second band of the same; p, pith. × 12. S. Coll. 457. (G. T. G.)

border of the pith, cannot be recognised with certainty in Nield's specimen, and if present, must, it would seem, have been much reduced. The remains of leaf-traces, passing out through the secondary wood, are seen at several places, but even here the primary xylem of the outgoing bundle has not been detected. It must

therefore remain an open question whether the primary structure of the xylem was of the *Lyginodendron* type, or whether the whole wood developed centrifugally, as in the stem of recent Cycads or Conifers. On the other hand, the large stem presents a peculiarity of structure which occurs in some specimens of *Lyginodendron oldhamium*. It was mentioned above (p. 372) that, in that plant, anomalous vascular tissues are sometimes developed in the outer part of the pith, immediately within the normal ring of bundles. These tissues, when present, have inverted orientation, the xylem facing outwards, towards the normal wood, and the phloëm inwards, towards the centre of the pith. Precisely the same anomaly reappears, in a more striking form, in *Cycadoxylon robustum*. There is a distinct zone of secondary wood at the margin of the pith, reaching in places a thickness of about sixteen tracheides in a radial row, and on the inner side of the anomalous zone, a corresponding band of phloëm can be recognised (Fig. 178, x^3, ph^3). Thus, the medullary vascular tissues had the same reversed orientation as in the corresponding anomalous formations sometimes found in *Lyginodendron oldhamium*. In *Cycadoxylon robustum* the anomalous vascular zone is at some places double, the second band of medullary wood and bast having the same orientation as the first (see Fig. 178, x^4, ph^4).

The structure as a whole leaves little doubt that the fossil *Cycadoxylon robustum* really possessed some affinity with *Lyginodendron*, but, as there is no proof that the primary structure of the two was similar, we no longer place them in the same family, but have trans-

ferred the species discovered by Nield to the type-genus of the Cycadoxyleae, to which, as we shall now see, it naturally belongs.[1]

The interest of the fossil depends on two points. The first is the thoroughly Cycadean character of the secondary wood, a character shown much more evidently in this large stem, which in its dimensions is comparable to that of a recent Cycad, than in the smaller stems of the Lyginodendreae. The second point is the marked development of the anomalous medullary vascular tissues, which we have already found, as an individual peculiarity, in *Lyginodendron oldhamium*.

A small stem, from the Lower Permian of Autun, described by M. Renault, and named *Cycadoxylon Fremyi*, shows still more perfectly the type of structure just described. The stem is from 20 to 25 mm. in diameter; the cortex, which is fairly preserved, contains gum-canals, and large pitted elements, probably with a mechanical function. Within the cortex is a ring of normal wood and bast, both well preserved, and exactly resembling the vascular tissue of a modern Cycad. The medullary rays are extremely wide, exceeding in extent the tracheal bands between them. The tracheides are for the most part pitted; the bordered pits are ranged in numerous series on the radial walls. Towards the interior of the normal zone of wood, scalariform

[1] On *Cycadoxylon robustum*, see Williamson, "Organisation of the Fossil Plants of the Coal-measures," Part iv., *Phil. Trans.* 1873, p. 386; Williamson and Scott, "Further Observations," etc., Part iii., *Phil. Trans.* vol. 186, B, 1895, p. 742; Seward, "A Contribution to our Knowledge of *Lyginodendron*," *Annals of Botany*, vol. ix. 1897, p. 65.

As Professor Seward points out, the specimen described by M. Renault in the *Flore fossile d'Autun et d'Epinac*, Part ii., under the name of *Medullosa gigas*, appears to be almost identical with Nield's plant.

tracheides occur, and at its inner limit are the spiral elements of the protoxylem. It would thus appear that the whole normal wood was centrifugally developed, as is usual in recent Cycads. Professor Seward, however, states that at one place he detected a distinct strand of primary xylem ; this may indicate that some trace of the mesarch structure of the Lyginodendreae still persisted in *Cycadoxylon*, though much reduced. The wide phloëm-zone consists of alternating concentric bands of parenchyma and sieve-tubes.

Within the normal vascular ring, are two or more interrupted zones of anomalous wood and bast, with inverted orientation, the phloëm facing inwards. These medullary vascular arcs are separated by parenchyma from the normal centrifugal wood. The whole structure is thus comparable to that of *Cycadoxylon robustum*, except that the normal zone is much less developed, which may simply be a matter of age.

Curiously enough, no leaf-trace bundles have so far been found in *Cycadoxylon Fremyi*. The characters, as at present known to us, strongly suggest Cycadean affinities, though the characteristic anomaly of *Cycadoxylon*, the formation of inverted zones of secondary wood and bast in the pith, is not known in the same form among recent Cycads. On the other hand, it is identical with the most frequent anatomical variation occurring in stems of *Lyginodendron oldhamium*.

Another silicified stem from the Permian of Autun, the *Ptychoxylon Levyi* of M. Renault, presents a somewhat similar combination of characters. In this fossil the dimensions are greater than in *Cycadoxylon Fremyi*, the stem of *Ptychoxylon* attaining a diameter of 5 or 6

cm. The external surface bears the marks of spirally disposed appendages. The character of the genus depends on the arrangement of the vascular tissues.

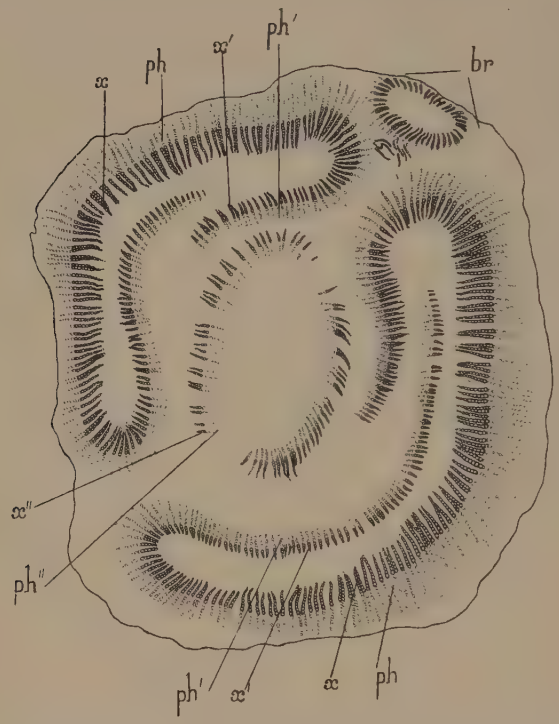

FIG. 179.—*Ptychoxylon Levyi*.—Transverse section of a decorticated stem. *x*, *ph*, normal xylem and phloëm; *x'*, *ph'*, first inverted medullary bands of xylem and phloëm, continuous at the leaf-gaps with the normal zone; *x''*, *ph''*, second inverted zone; *br*, stele of a branch. Slightly magnified. After Renault.

There is an outer, more or less continuous cylinder of wood and bast, surrounding a very large pith, within which are several secondary vascular bands, with their wood developed centripetally, while that of the normal outer ring is centrifugal (Fig. 179). The traces of both

leaves and branches are present, and, as the two organs appear to correspond in position, it is not improbable that the latter were axillary. It seems that the phyllotaxis was $\frac{3}{8}$.

Where the bundles of a leaf or branch pass out, the external vascular cylinder is interrupted, and its edges are incurved, to unite with two of the internal vascular bands (see Fig. 179, *x'*, *ph'*). The latter are thus always continuous, at some point of their longitudinal course, with the normal vascular ring. This, it will be remembered, is precisely what happens in some specimens of *Lyginodendron oldhamium*, where the anomalous medullary wood and bast are likewise connected, at the leaf-trace gaps, with the normal vascular tissues (see p. 372). In *Ptychoxylon*, however, the conditions are more complicated, for there are often two or three concentric systems of internal vascular arcs, joining on at different levels, to the external ring (see Fig. 179, *x''*, *ph''*).[1] The character of the wood and bast of each ring is very parenchymatous, like that of *Cycadoxylon*, or of a recent Cycad. The phloëm, which is external in the case of the normal zone, but internal in each of the anomalous bands, is beautifully preserved, and even the details of the sieve-tubes have been made out. There appears to be no indication in this genus of any primary centripetal wood in the stem.

The leaf-traces, however, appear, from M. Renault's description and figures, to have essentially the same structure as in *Lyginodendron*; the trace consists of two bundles, side by side; in each bundle there is a large

[1] Compare the double anomalous zone in *Cycadoxylon robustum*, Fig. 178.

arc of secondary wood on the outer side of the primary strand; the spiral elements lie near the limit of primary and secondary wood, so it appears that the former was wholly or mainly centripetal in its development.

The parenchymatous cortex, which contains secretory sacs, or canals, is coated externally by periderm; this may account for the absence of any hypodermal fibres, which had very probably been lost by exfoliation.

The branches, at their base, had a normal vascular ring, but as they became free, gradually assumed the complex structure of the main stem.[1]

The stems just described, *Cycadoxylon robustum*, *C. Fremyi*, and *Ptychoxylon Levyi*, may be grouped under the family-name of Cycadoxyleae, a designation already used by M. Renault, but in a somewhat more extended sense.[2] The interpretation of their structure, which, in agreement with the views of Professor Seward,[3] I desire to suggest, is that they may have been derived from some form resembling *Lyginodendron oldhamium*, from which they have deviated in two principal respects. On the one hand, they have gradually lost the *primary* centripetal wood of the vascular bundles in the stem. In *Cycadoxylon robustum*, this tissue has not been recognised with certainty, and must at most have been relatively unimportant; in *C. Fremyi* it was certainly on the verge of extinction; in *Ptychoxylon* it had

[1] For a full description of *Cycadoxylon* and *Ptychoxylon*, see Renault, *Bassin Houiller et Permien d'Autun et a'Epinac, Flore fossile*, Part ii. pp. 307-21, 1896.

[2] M. Renault includes *Medullosa* and *Colpoxylon* in the Cycadoxyleae. On the view here taken, these two genera belong to a different, though related, line of descent, as has already been shown.

[3] "Contribution to our Knowledge of *Lyginodendron*," *Annals of Botany*, vol. xi. 1897.

probably disappeared altogether. This change is in a Cycadean direction, for the recent Cycads (as well as the Mesozoic Bennettiteae) have wholly lost the centripetal primary wood of their vegetative stems, while retaining it in their leaves, and occasionally in the peduncles of their cones. It is very interesting to find that the leaf-trace bundles in the cortex of *Ptychoxylon* retain the *Lyginodendron* structure: in a typical Cycad they would not possess centripetal wood in this part of their course.

The extinction of the centripetal xylem was, no doubt, correlated with the advance of secondary growth. As the centrifugal wood became more and more predominant, with the increasing activity of the cambium, the small centripetal portion (the "Cryptogamic" wood of the French authors) became insignificant in comparison, and could be dispensed with, so far as the stem is concerned. In the roots there was a special physiological reason, connected with the absorptive function, for its retention,[1] and here it has held its own all through; in the leaves, where secondary tissue-formation is less marked, it persisted in many cases, as in Cycads, Cordaiteae, and perhaps Coniferae, but in the highly modified sporophylls, even of Cycads, it tends to disappear.[2]

On the other hand, the Cycadoxyleae became modified in another direction, and one peculiar to themselves among the allied groups. The anomalous formation of inverted medullary wood and bast, which in *Lyginodendron* only appears as an individual and

[1] See Strasburger, *Histologische Beiträge*, iii. p. 140.

[2] See Worsdell, "Vascular Structure of the Sporophylls of the Cycadaceae," *Annals of Botany*, vol. xii. 1898.

comparatively unimportant peculiarity, had in the Cycadoxyleae grown to be a constant and marked character. We regard this structure as a new formation, due to the spreading inwards of cambial divisions through the leaf-trace gaps, as is clearly shown in *Lyginodendron* itself, and in *Ptychoxylon*. There is no reason to suppose that the anomalous centripetal wood thus formed had anything to do with the primary and normal centripetal wood of the more primitive forms: the example of *Lyginodendron oldhamium* shows that the two structures were quite independent. Neither does it seem practicable to derive the structure of Cycadoxyleae from a system of Medullosean steles. Scattered medullary bundles are a characteristic anatomical feature in the recent genera *Encephalartos* and *Macrozamia*,[1] but continuous zones or extensive arcs of inverted wood and bast do not appear to be known in the pith of undoubted Cycads. Such anomalies, however, as shown by similar cases in many recent Dicotyledons, are extremely variable, and the peculiarity in question cannot hinder us from recognising the essentially Cycadean character of the stems of Cycadoxyleae.

It must always be remembered that the Cycadophyta were once an extensive and dominant class of plants, and that the few, which have survived to our own time, only give us a very imperfect and partial idea of the range of organisation which the group once exhibited (see Chap. XIII.).

It is interesting to find that the same Permian beds of Autun, which have yielded the stems of Cycadoxyleae,

[1] See Worsdell, "Anatomy of the stem of *Macrozamia*," etc., *Annals of Botany*, vol. x. 1896. "The Structure and Origin of the Cycadaceae," *ibid.* vol. xx. 1906.

also contain both leaves and fructifications which may be of a Cycadean character. The leaves are referred to the genera *Pterophyllum* and *Sphenozamites*,[1] the former recalling the foliage of the recent *Dioon*, and the latter that of some species of *Zamia*. The agreement, in form and venation, with typical Cycadean leaves, is sufficiently close to render it probable that the affinities of these fossils were with the Cycadophyta.

The fructification referred to—*Cycadospadix milleryensis*, Ren.[2]—is a very remarkable one, represented in Fig. 180. The axis bears numerous fimbriated sporophylls (*l*), concave on their lower surface, and on the under side of each sporophyll two seeds (*s*) were borne. M. Renault, the discoverer, states that the sporophylls are spirally arranged, and regards the whole structure as constituting a lax cone. Some of the specimens are inserted, almost at right angles, on a branch little thicker than the axis of the cone itself. Such an arrangement is not found among true Cycads, but the com-

FIG. 180.—*Cycadospadix milleryensis*. Fructification, consisting of an axis, bearing numerous laciniate sporophylls (*l*), each of which bears seeds (*s*) (probably two to each sporophyll) on its lower surface. Slightly reduced. After Renault.

[1] See Renault, *Flore fossile d'Autun et d'Epinac*, Part ii. [2] *Loc. cit.*

paratively slender, branched stem of the Rhaetic *Anomozamites* (see Chap. XIII.) offers an analogy, and as *Ptychoxylon*, at any rate, is known to have branched pretty freely, it is quite possible that M. Renault's interpretation is the right one. It seems not impossible, however, that the whole structure may represent a single compound leaf or sporophyll, or even a single fertile pinna, the bodies immediately bearing the seeds being of the nature of leaflets. In the latter case, we should have a sporophyll more complex than that of any recent Cycad, and its affinities would probably be with the Pteridosperms; on M. Renault's interpretation, the fructification would represent a nearer approach to the cones of the Zamieae. In any case the fossil is of the greatest interest, and it is much to be hoped that specimens with structure preserved may yet be discovered.

Whether these leaves and fructifications belonged to Cycadoxyleae or not, it is probable that the stems in question (or some of them) were those of plants which had already passed the boundary (at most a very indefinite one) between Pteridosperms and Gymnosperms.

Protopityeae

The Lyginodendreae, Calamopityeae, and Cycadoxyleae appear to form one group, though by no means a linear series. The next type of Cycadofilices to be considered is represented by a remarkable and isolated form, our present knowledge of which is due to the investigations of Count Solms-Laubach. This is the *Protopitys Buchiana* of Göppert, a very ancient fossil,

derived from a Lower Carboniferous or possibly Devonian horizon at Falkenberg, in Silesia.[1]

The stem attained a great thickness; one of the specimens was almost a foot and a half in diameter. The greater part of this thickness is made up of the secondary wood, which has the general structure of Cordaitean or Coniferous wood, consisting of tracheides and small medullary rays, the latter usually one or two cells in thickness, and from one to eight or ten cells in height. The bordered pits, however, which are limited to the radial walls of the tracheides, are transversely elongated, and are thus intermediate between the scalariform type and the usual Pteridospermous or Gymnospermous form of pit. The secondary bast is preserved in some cases, and proves to have consisted of alternating zones of sieve-tubes and stone-cells. The primary part of the structure is in striking contrast with that of the secondary region. The middle of the stem is occupied by a large elliptical pith, surrounded by a zone of primary wood, of very unequal thickness, but continuous, and not broken up into distinct bundles. On the sides of the ellipse, the primary xylem thins out to a width of from one to three elements only, but at the ends it is greatly thickened, and, in this part, xylem-parenchyma is intermixed with the scalariform primary tracheides. It was from the ends of the elliptical stele, that the bundles passed out to the distichously arranged leaves. The leaf-traces were of large size, and forked immediately on becoming free from the xylem-ring. The gap, left in the latter by the departure of the leaf-trace, was gradually filled by the enlargement and

[1] Solms-Laubach, *Botanische Zeitung*, 1893, p. 197.

coalescence of the adjacent edges of the interrupted zone of primary wood. It is only in this region, that any indication of protoxylem-elements has been detected.

The stem gave off branches, of much smaller size than the main axis. The whole structure is quite peculiar: the arrangement of the primary tissues points clearly to Filicinean affinities, while the secondary tissues have a Gymnospermous, though by no means a specially Cycadean, character. The organisation departs widely from that of the Lyginodendreae, notably in the distichous arrangement of the leaves. We can only agree with Count Solms, in regarding this plant as the representative of a distinct family, forming one more of those Palæozoic types which combine the characters of Filicineae and Gymnosperms. *Protopitys* is thus an isolated genus, the relation of which to the other groups described in this chapter is doubtful, though its provisional place is clearly among the Cycadofilices.

Another species has since been discovered by Mr. Kidston in the Yoredale Rocks of Yorkshire, but has not yet been described.

Cladoxyleae

Before leaving the Cycadofilices, it will be well to refer shortly to an interesting group of early Palæozoic plants, which have long been known, but the true structure of which was only cleared up in 1897, by the investigations of Count Solms-Laubach.[1]

The fossils in question, belonging to the genus *Cladoxylon* of Unger, were found in Thuringia, at the

[1] "Pflanzenreste des Unterculm von Saalfeld," above cited.

same horizon and locality which yielded the specimens of *Calamopitys Saturni*, described above. Their age is now considered to be Devonian. They are fragments of stems, referred to several so-called species, but agreeing in the fact that they have a complex, polystelic structure. In *Cladoxylon mirabile* the steles are much elongated, as seen in transverse section, often curved and sometimes fusing with one another, their long axis usually lying in the radial direction. In *C. dubium* they are shorter and simpler in form. The point of interest is that in most of the specimens each stele has its own zone of secondary wood, while in other cases the primary structure has remained unaltered, thus presenting altogether the appearance of a polystelic Fern-stem. Both primary and secondary wood are made up of scalariform tracheides ; the secondary zone is traversed by numerous medullary rays. In the primary wood, one or more groups of spiral elements have been recognised, usually situated (according to the species) at one or both ends of the stele. In one case, an appendage, containing a single concentric bundle, was found in connection with the stem, and was no doubt of the nature of a petiole. The general organisation is clearly comparable to that of a *Medullosa*, though there are many differences in detail. It is certainly interesting to find, that this remarkable combination of polystelic organisation with secondary growth had already appeared at so ancient a period as that of the Devonian.

It is not probable that the relation between the Cladoxyleae and the Medulloseae was at all a close one, for the differences in the minute structure of the wood,

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and in the organisation of the petiole, as well as in the arrangement of the steles, appear to be of considerable weight. The two families probably represent parallel lines of development.

A comparison has been suggested between the complex system of steles in *Cladoxylon* and the deeply lobed and forked stele of *Asterochlaena* (see Vol. I. p. 324), and it is possible that there may be a real affinity between the two groups.

There are other types of Cycadofilices still undescribed; one of these may be shortly referred to, though its affinities cannot yet be determined. This stem comes from the Lower Carboniferous of the Tweed; the first specimen was discovered by Mr. Mathieson in 1871; within the last few years additional material has been collected by Mr. Kidston, who has the fossil under investigation; it has been named *Stenomyelon tweedianum*, Kidston in MS. The primary wood consists of a mass of tracheides, continuous except where it is traversed by bands of parenchyma, which may be regarded as forming a narrow and irregular pith. The position of the protoxylem appears to have been external. The secondary wood is of considerable thickness, and has a rather dense structure, with narrow medullary rays. The tracheides are mostly of the usual multiseriate-pitted type, though transitional scalariform elements occur near the protoxylem. The outer cortex has the common strengthening-bands of sclerenchyma; numerous leaf-trace bundles lie between wood and cortex, and there is some evidence that they arose by the subdivision of a smaller number of main strands.

A distant resemblance to the structure of *Sutcliffia* may be traced, but we must await the results of further investigation before forming any opinion as to the true relationships of the fossil.

The question of the relation of the families still provisionally grouped under Cycadofilices to the Seed-plants on the one hand and to the Ferns on the other, must necessarily remain an open one so long as any satisfactory evidence as to the fructification is absent. In the case of the Calamopityeae and Cycadoxyleae the high anatomical organisation affords a presumption that we here have to do with Pteridospermeae, even if not with more advanced Spermophyta; the analogy between the structure of *Megaloxylon* and that of *Heterangium* among the Lyginodendreae points, though much less decidedly, in the same direction. The Protopityeae and Cladoxyleae, however, appear too isolated, at present, for us even to venture on any conjecture as to their affinities, beyond what is implied in classing them as "Cycadofilices."

CHAPTER XII

THE CORDAITALES

Poroxyleae ; Pityeae ; Cordaiteae

I. Poroxyleae

We now pass on to a group of fossil plants, which occupies a somewhat different position from those which we have just described. The latter were found, on the whole, to combine the characters of the Ferns with those of the great Cycadophytic stock, and might thus be regarded as indicating the probable derivation of the latter from the former. The group next to be considered, that of the Poroxyleae, while having much in common with certain of the Pteridosperms and Cycadofilices, especially with the Lyginodendreae and Calamopityeae, show affinities not so much with the Cycadophyta as with a wholly extinct order of Gymnosperms, the important Palæozoic family Cordaiteae. The three families, Poroxyleae, Pityeae, and Cordaiteae, are, in fact, so interrelated that they may best be united under the common class-name Cordaitales.

The Poroxyleae are represented at present by the one genus *Poroxylon* (of which two or three species are

known). *Poroxylon* is a genus in which the available data chiefly relate to the vegetative structure; such evidence as we possess concerning its organs of reproduction will be considered later on. Our present, very complete knowledge of the anatomical structure, which is preserved in astonishing perfection, was due in the first instance to the investigations of the two French palæobotanists, MM. Renault and Bertrand.[1]

The genus was originally discovered in the Permo-Carboniferous deposits of Grand Croix and Autun, in France; an allied species has recently been recorded from the Lower Coal-measures of Lancashire.

The two best-known French forms, *Poroxylon Boyssetii* (which includes the specimens first discovered, and described by M. Renault in 1879) and *P. Edwardsii*, only differ from each other in unimportant characters, which may or may not be of specific value.

The stems of these plants were comparatively slender, the specimens described not much exceeding half an inch in diameter; they bore spirally arranged leaves, separated from each other, for the most part, by rather long internodes; the French authors have worked out the phyllotaxis, from the course of the leaf-trace bundles, and found the divergence between two successive leaves to be $\frac{5}{13}$. The leaves themselves were very different in character from those of any of the Pteridosperms, as at present known. They were broad, thick, simple leaves, inserted on the stem by a definite petiole, and tapering towards the opposite extremity. The lamina

[1] Renault, *Tiges de la flore carbonifère*, 1879; Bertrand et Renault, "Les *Poroxylons*," in *Archives bot. du Nord de la France*, 1886.

was traversed by numerous parallel veins.[1] This is quite a different type of leaf from anything we have met with among the groups already considered.

The structure of the stem, however, is of a type already familiar to us. The transverse section of a young stem is represented in Fig. 181, B. We see at once that there is a well-marked pith, surrounded by a ring of collateral vascular bundles. The primary xylem-strands of these bundles, which border immediately on the pith, are clearly marked off from the surrounding zone of radially arranged secondary wood, which is succeeded externally by the well-preserved cambium and phloëm. The stem thus had secondary growth in thickness, of a normal character. The pericycle, immediately surrounding the phloëm, and the inner primary cortex, contain structures interpreted as gum-canals, and similar organs are also present in the pith. The outer cortex was strengthened by a system of hypodermal strands of sclerenchyma, such as we have so often met with in the stems of Palæozoic plants. The general anatomy of the stem is thus strikingly similar to that of a *Lyginodendron*, and a more detailed examination shows that the resemblance is a real one. A general agreement with *Calamopitys* is also evident.

The bundles surrounding the pith are rather more numerous than in *Lyginodendron*, a fact which is correlated with the more complex phyllotaxis of

[1] The leaves, or at least their laminae, do not appear to have been found in connection with the stem, in these species, but as MM. Bertrand and Renault pointed out, the close anatomical agreement between stem and leaf established a strong presumption that the two organs belonged to identical or closely related species. In the British species, *P. Sutcliffii*, the connection between the stem and leaf-bases is clear.

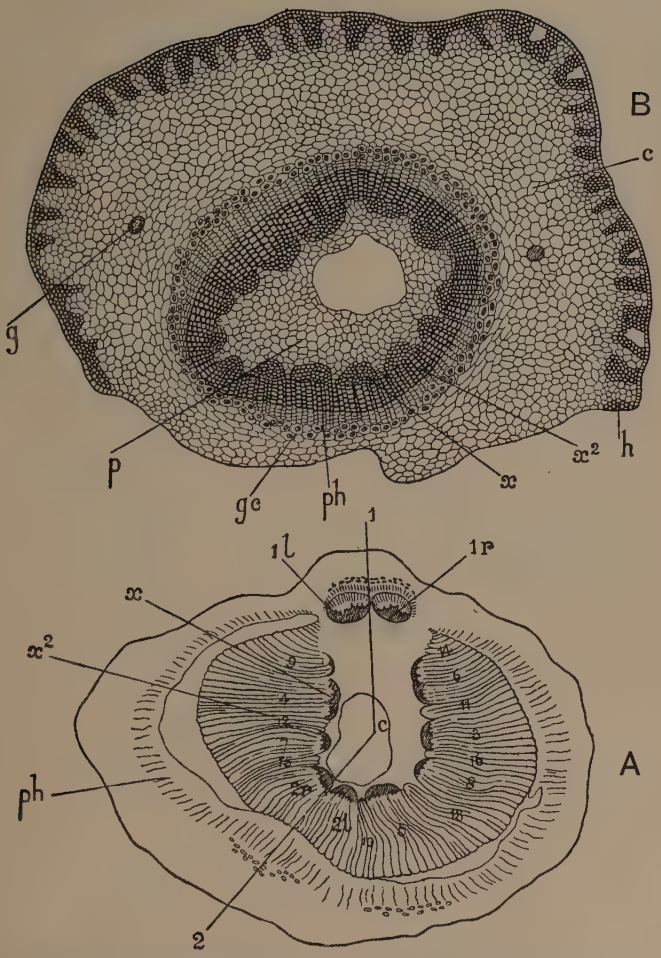

FIG. 181.—A, *Poroxylon Edwardsii*. Transverse section of stem. *c*, cavity in pith; *x*, primary wood of bundles, which are numbered in the order of the $\frac{5}{13}$ phyllotaxis, No. 1 belonging to the lowest leaf of the series; the angle 1, *c*, 2, is that of the divergence between two successive leaves; 1*l* and 1*r*, the two bundles constituting the outgoing leaf-trace; x^2, secondary wood; *ph*, phloëm. × about 5. After Bertrand and Renault. B, *P. Boyssetii*. Transverse section of young stem. *p*, pith; *x*, primary wood of bundles; x^2, secondary wood; *ph*, phloëm; *gc*, secretory (?) sacs or canals; *g*, mucilage-canal; *c*, cortex; *h*, hypoderma. × 7. After Renault.

Poroxylon. Each leaf-trace, on entering the stem from a leaf, runs down through thirteen internodes, before joining the trace of a leaf vertically below. Hence, in any transverse section of the stem, the traces of thirteen successive leaves are met with (see A, Fig. 181).

The internodes are long, and as the leaf-trace traverses the cortex in about half the length of an internode, it follows that in any transverse section of the stem not more than one outgoing trace (if any) is shown (see Fig. 181, A and B). Each leaf-trace, in the upper part of its course, consists of a double bundle. It will be remembered that in *Lyginodendron* also the leaf-trace is a double one. In that genus, however, the two strands of the trace unite, as we follow them inwards through the pericycle (see Fig. 129, p. 359); in *Calamopitys* they unite in the same region (Fig. 176), whereas in *Poroxylon* they remain distinct for some distance below their entry into the interior of the stele. Thus, the two strands of primary wood shown in Fig. 182 both belong to the same leaf-trace, which (proceeding from the second leaf above) has already taken up its position at the margin of the pith.

This figure also serves to illustrate the important point that the development of the primary xylem of the bundles was *centripetal.* At the level of the section each of the twin-bundles has two protoxylem-groups (*px*), separated by parenchyma from the secondary wood on their exterior side. The centripetal xylem of each strand forms an arc, abutting, at its ends, on the secondary wood. The whole structure is strikingly like that in *Lyginodendron* (cf. Fig. 131, p. 364), except

that, according to the observations of MM. Bertrand and Renault, there is no centrifugal primary xylem in the case of *Poroxylon*. This is a point which might repay further investigation.

The elements adjoining the spiral protoxylem are scalariform, while the more internal part of the centri-

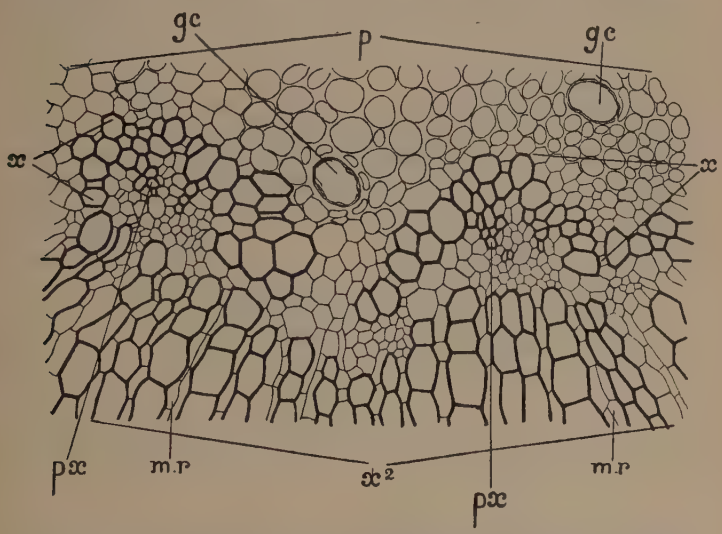

FIG. 182.—*Poroxylon Edwardsii*. Transverse section of the stem, showing two primary xylem-strands, with adjacent tissues. *p*, pith; *gc*, mucilage-canals; *px*, protoxylem; *x*, primary centripetal xylem; x^2, secondary xylem; *m.r*, medullary rays. × 66. After Bertrand and Renault.

petal wood consists of pitted elements, exactly as in *Lyginodendron* or *Heterangium*. Traced further downwards in the stem, the structure of the primary wood becomes simplified; the protoxylem-groups fuse with each other, and ultimately die out. It is a fact well known to anatomists that the spiral elements often disappear in the lower part of the course of a bundle, as is very clearly seen in the Fern *Osmunda*, the

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structure of which is in many respects comparable to that of the plants under consideration. Eight internodes below the node the centripetal xylem also disappears, leaving only the wedge of secondary wood to mark the position of the trace (see Fig. 181, A, bundles 10-14; cf. *Calamopitys Beinertiana*, p. 482). The communication between the different leaf-traces was kept up by lateral fusions, during their passage down the stem.

The secondary wood presents no peculiarities; it consists of regular, radial series of tracheides, with medullary rays between them. The rays are of considerable height, and two or three cells in thickness; the tracheides have several rows of round or hexagonal bordered pits on their radial walls. The structure, in fact, is identical with that of the wood in *Lyginodendron*, so that the two could scarcely be distinguished.

The secondary phloëm, which is extraordinarily well preserved, is traversed by the medullary rays, and made up of alternate tangential bands of sieve-tubes and parenchyma. *Poroxylon* is one of the few fossil plants in which the structure of the sieve-tubes can be made out. A radial section of *P. Edwardsii* is figured by MM. Bertrand and Renault, in which the numerous compound sieve-plates on the radial walls are perfectly plain, just as in some recent Cycads. *Heterangium tiliaeoides*, *Medullosa anglica*, and *Stauropteris oldhamia*, among British fossil plants, sometimes rival *Poroxylon* in the perfection with which the phloëm is preserved.

The French authors state that there is no pericycle, distinct from the primary phloëm. That is a matter of interpretation, but it is an interesting point that the

formation of periderm took place on the inner border of the cortex, and immediately outside the "primary phloëm"—in fact, in just the same position which it occupied in *Lyginodendron*. In the older stems, the whole of the cortex was thrown off as bark, a stage which has not been observed in the latter genus, though *Calamopitys* may offer analogies.

The double leaf-trace, as it passes out through the cortex, preserves its collateral structure, and is accom-

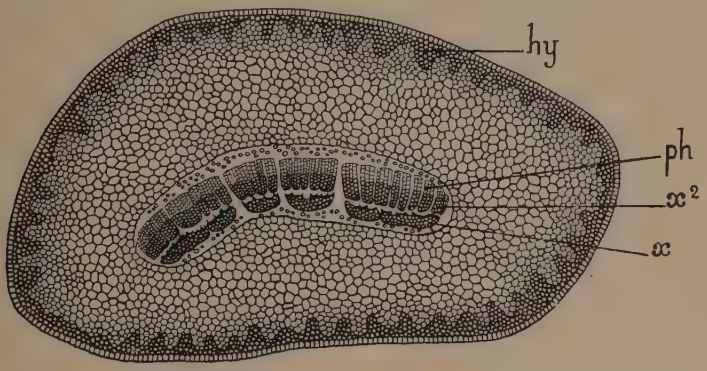

FIG. 183.—*Poroxylon Boyssetii*. Transverse section of petiole. *x*, primary xylem; x^2, secondary xylem; *ph*, phloëm; *hy*, hypoderma. × about 10. After Renault.

panied by secondary wood and bast on its outer side. The same structure is maintained in the leaf itself. Fig. 183 represents a transverse section of the petiole of *P. Boyssetii*. The vascular bundles, which have begun to subdivide, are arranged in a transverse series, the phloëm facing downwards and the xylem upwards, as is usual in leaves; they present essentially the mesarch structures of the bundles of Cycadean leaves (cf. Fig. 133, p. 365). The petiole, like the stem, had a strong mechanical construction, owing to

the presence of hypodermal ribs of sclerenchyma (Fig. 183, *hy*).

The petiole widened out gradually into the broad simple lamina, which was traversed by numerous parallel bundles, derived from the subdivision of those of the petiole, and branching dichotomously. The larger bundles, which are crowded together in the median region of the lamina, have the same structure as those in the petiole; the finer strands, toward the edges of the leaf, are simplified, and no longer show any centrifugal wood. Just the same simplification of structure occurs in the smaller bundles of the leaf, in recent Cycads. The lamina was of considerable thickness, and was stiffened by the usual hypodermal fibrous strands on both surfaces. The dense mesophyll is said to show some traces of palisade-like arrangement. The larger bundles of the lamina were connected by transverse bridges of thick-walled elements.

M. Grand'Eury[1] has recently identified the leaves of *Poroxylon* in the form of carbonaceous impressions. He finds that they are of great size, reaching a length of a metre, with a breadth of ·15 to ·20 metre. They are narrowed at the base, passing insensibly into the petiole.

In these leaves we have a highly remarkable organisation, totally different from anything met with, either in the Ferns themselves, or among the genera associated under the Pteridospermeae and Cycadofilices. The detailed structure is, in fact, that of a Cycad, but the leaf of *Poroxylon* was a simple, not a compound

[1] "Sur les *Rhabdocarpus*, les graines et l'évolution des Cordaïtées," *Comptes Rendus*, t. cxl. p. 995, 1905.

one, so that the whole leaf has been compared to a single leaflet of a Cycad such as *Bowenia.*

In the fact that the vascular bundles retain collateral structure throughout the leaf, *Poroxylon* agrees with *Medullosa* but differs strikingly from *Lyginodendron*, in which, as described above (pp. 367 and 375), the structure becomes concentric as the petiole is entered. We shall see presently that the leaves of *Poroxylon* present the closest analogies with those of the Cordaiteae.

An interesting point in the morphology of the genus *Poroxylon* is the fact that the stem bore axillary branches, thus presenting a further analogy with some forms of *Lyginodendron.* The vascular system of the branch was inserted on the two bundles of the main axis, between which the trace of the subtending leaf passed out. Thus, in the section shown in Fig. 181, A, the branch, if present, would have been in vascular connection with the bundles marked 6 and 9. The first few internodes of the branch were short, and the first leaves probably rudimentary, judging from the small development of the leaf-traces supplying them. In its upper part, the branch assumed the same structure as the main stem.

Poroxylon appears to have possessed a complex branch-system, for shoots are found of very different calibre, independently of differences due to age.

Roots and rootlets, which have been found in association with *Poroxylon Boyssetii* and *Edwardsii*, agree so exactly, in the structure of their histological elements, with the stems of those plants, as to leave no reasonable doubt that MM. Bertrand and Renault

were justified in referring them to the genus *Poroxylon*. The rootlets, in particular, are perfectly preserved, and their anatomy has been fully investigated. The structure is, as a rule, diarch; in a few cases a tetrarch cylinder has been observed. The anatomy of the roots and rootlets is, in all respects, such as characterises Gymnospermous roots at the present day. In the usual case of diarch organisation, the secondary wood and bast form two large masses, one on either side of the primary xylem-plate, while a broad ray corresponds to each of the two protoxylem-groups at the ends of the plate. In the details of wood and phloëm the roots agree precisely with the stem. The whole cortex was thrown off at an early stage by the formation of pericyclic periderm. Thus the outer surface of the root was formed by a layer of cork, just as in the roots of *Medullosa anglica*, described in the last chapter, or in those of recent Gymnosperms.

MM. Bertrand and Renault were able to observe the mode of insertion of the rootlets on the main root, and to determine that the plane of the diarch xylem-plate coincided in the two organs. This is a point of interest, for, as is well known from the researches of Professor van Tieghem and others, this arrangement is characteristic of the roots of Gymnosperms and Phanerogams generally, while, in the case of the diarch roots of Vascular Cryptogams, the plane of the xylem-plate of the rootlet lies at right angles to that of the parent root.

Our summary has so far been based on the species discovered by Bertrand and Renault; the anatomy

was worked out in the most elaborate detail by the French investigators, owing to whose labours this genus became one of the most completely known, so far as the vegetative organs are concerned, among fossil plants.

An English species, of older date than the French

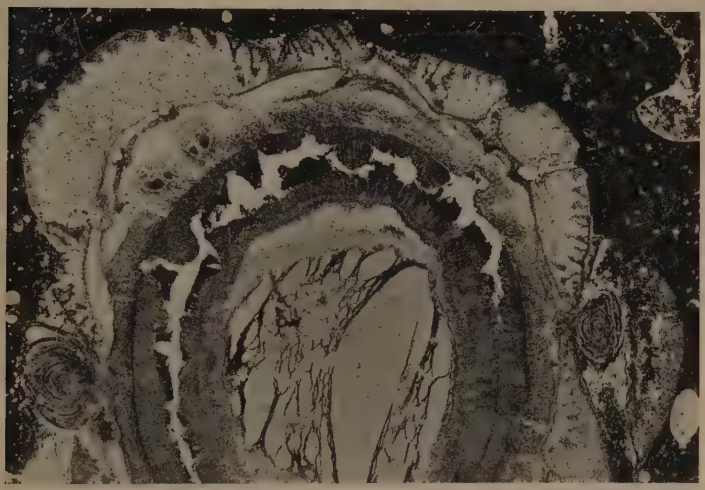

FIG. 184.—*Poroxylon Sutcliffii*. Transverse section of stem, showing the large pith, the ring of wood and phloëm, and the cortex, with leaf-bases attached, into which the leaf-traces are entering. Two axillary buds are shown; the one to the right is accompanied by the subtending leaf-base. × nearly 4. From a photograph by Mr. L. A. Boodle. Scott Collection.

forms, was found a few years back by Mr. Lomax, in a roof-nodule from the Lower Coal-measures of Shore-Littleborough, Lancashire; the species has been named *Poroxylon Sutcliffii* (Fig. 184), after the owner of the mine, to whose co-operation palæobotanists owe so much; though the plant is certainly related to the French Poroxylons, its place in the same genus must

be regarded as provisional, until the investigations now in progress are completed. The main features of the structure are the same as in the species already described; the primary strands of centripetal wood, the double bundles passing out from the pith, the cortical structure and the axillary branching are obvious points of similarity. The subdivision of the leaf-trace pairs, first into four and then into six strands, as they pass through the cortex, is particularly well shown, as are also the small axillary buds (Fig. 184). The leaves were evidently much more crowded on the stem than in the French type; the secondary wood is denser, with smaller tracheides and narrower rays; the pith is discoid, like that of *Cordaites*; the phloëm also has some peculiarities; it is thus probable that the distinctions existing may prove to be of generic value. In any case, the discovery of the *Poroxylon* type of stem at an horizon considerably lower than that of the species originally described, is one of much interest.

Until recently we were quite in the dark as to the fructification of *Poroxylon*. On grounds of association, however, M. Grand'Eury[1] now attributes the seeds known as *Rhabdocarpus*, Brongniart, to these plants, with which he also finds "floral axes, bearing large and long male and female buds, without bracts." *Rhabdocarpus*, as limited by Brongniart, is a genus of seeds with bilateral symmetry, characterised by the presence of numerous fibrous strands in the sarcotesta. The seeds are of the same general type as those of the Cordaiteae, described below (see p. 546). Fig. 185 shows a seed of this genus in transverse section,

[1] See his paper above cited, "Sur les *Rhabdocarpus*," etc.

displaying the characters of the platyspermic type. The discovery, if confirmed, will considerably strengthen the affinity otherwise indicated between the Poroxyleae and Cordaiteae.

MM. Bertrand and Renault regarded the genus as related, on the one hand, to *Sigillaria*, and, on the other, to Cordaiteae. The affinity with the Cordaiteae seems indisputable, as will appear when we come to describe that family; the relation to *Sigillaria*, however,

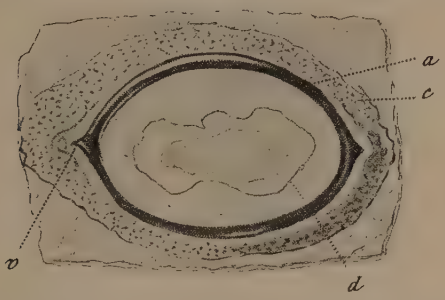

FIG. 185.—*Rhabdocarpus subtunicatus* Grand'Eury. Transverse section of seed, to show the platyspermic type of structure. *a*, sclerotesta; opposite the ridge (*v*) at each side is a vascular bundle; *c*, sarcotesta, with numerous fibrous strands; *d*, contracted nucellus, within which is the embryo-sac. × about 3. After Brongniart.

though it appeared tenable at the time it was suggested, and was supported by the case of *Sigillariopsis*, with its double foliar bundle and occasionally pitted tracheides (see Vol. I. p. 230), now seems to be excluded by the manifest affinity between *Poroxylon* and the Pteridosperms of the *Lyginodendron* group. As has already been pointed out, and as the French observers recognised, the agreement in structure between *Poroxylon* and *Lyginodendron* is in many respects a close one, so much so that there can scarcely be a doubt that the two genera are allied. The same remark applies, to

a great extent, to the Calamopityeae also. These Pteridosperms, however, as is now abundantly proved, had their nearest relationships with the Ferns, and the inference appears justified that *Poroxylon* also, though more modified, was derived from a Filicinean, rather than a Lycopodinean stock. The importance of this conclusion will become evident when the Cordaiteae have been considered.

II. The Pityeae

Before going on to the Cordaiteae we will shortly consider a group of fossil plants which, so far as our limited knowledge shows, appear to lead up to that family, and to form part of the wider group which we call Cordaitales.

Most of the stems in question fall under the genus *Pitys* of Witham,[1] as emended by Göppert.[2] There are three species, all from the Lower Carboniferous of Southern Scotland, and all described by Witham in his famous pioneer work of 1833. The species are chiefly distinguished by the width of the medullary rays, the principal rays being as much as seven cells wide in *P. primaeva*, five or six cells in *P. antiqua*, and four cells in *P. Withamii*. *Pitys Withamii* is the well-known Craigleith tree, of which a trunk is set up in the grounds of the Natural History Department of the British Museum. A stem of this species found at Craigleith, near Edinburgh, in 1830, was 47 feet in

[1] *The Internal Structure of Fossil Vegetables found in the Carboniferous and Oolitic Deposits of Great Britain, described and illustrated*, Edinburgh, 1833, p. 71.

[2] "Revision meiner Arbeiten über die Stämme der fossilen Coniferen," *Botan. Centralblatt.* Band v. and vi. 1881.

length; at the top, the wood still had a diameter of $1\frac{1}{2}$ feet.

The pith and wood are the only parts preserved in any of the species, as at present known. The wood, except for the greater width of the principal medullary rays, is of the Araucarian type, and thus, as we shall see, agrees with that of the Cordaiteae (cf. Fig. 190, p. 528); the secondary tracheides have multiseriate bordered pits, confined for the most part, to their radial walls.

The point of chief interest is the presence, in all three species, of a number of small strands of primary wood, disposed around the pith.[1] This structure is best shown in *Pitys antiqua*, the Lennel Braes tree, from which the illustration in Fig. 186 is taken. The imperfectly discoid pith is large, sometimes as much as 2 inches across; in a specimen where the pith measured only 22 mm. in diameter, the number of xylem-strands round the pith was between forty and fifty. The diameter of each xylem-strand is small, averaging about ·25 mm.; most of the strands are embedded in the pith at some little distance from the inner edge of the woody zone (Fig. 186), with which they only come into contact when about to make their exit as leaf-traces. Where a xylem-strand passes out into the zone of secondary wood, its place is taken by a reparatory strand lying behind it, deep in the pith. The outgoing strand shows some sign of division into two, but the two halves appear to reunite further out in its course.

[1] Scott, "Primary Structure of certain Palæozoic Stems," etc., *Trans. Roy. Soc. Edinburgh*, vol. xl. Part ii. 1902.

Branching and anastomosis of the strands are found at many places.

In the great majority of the xylem-strands the structure is definitely mesarch, the spiral protoxylem-elements lying in the interior (Fig. 186, *px*). The

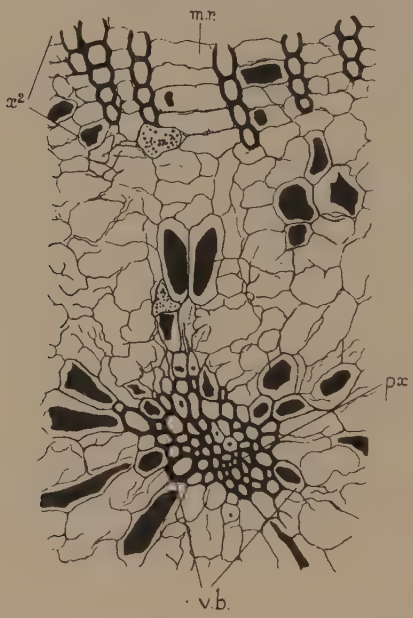

FIG. 186.—*Pitys antiqua*. From a transverse section of the stem. *v.b*, primary xylem-strand embedded in the pith; *px*, protoxylem; x^2, inner part of secondary wood; *m.r*, medullary rays. The cells with black contents may be secretory sacs. × 73. Kidston Coll. 598A. (G. T. G.)

primary tracheides are accompanied by a little xylem-parenchyma.

No spiral elements could be detected at the inner edge of the woody zone, so it would appear that the primary wood is represented only by the medullary strands. The considerable separation between the latter

and the main zone of wood is difficult to account for, and suggests some specialisation of function, as, for example, that the primary strands might have become superfluous for the main work of water-conduction and have served to supply the bulky parenchymatous pith.

The mesarch xylem-strands, in spite of their reduced size and the peculiarities of their arrangement, are evidently comparable to those of the Lyginodendreae and Calamopityeae. On the other hand, the arboreal habit suggests affinity with the Cordaiteae; leaves and seeds attributed to this family have been found in beds of the same age. Thus it is probable that the *Pitys* trees may form a link between the Pteridospermeae and the true Cordaiteae, though their position cannot be finally determined until we have a more complete knowledge of their structure.

In connection with *Pitys* another stem may be mentioned, which is of some interest from the same point of view. This is *Dadoxylon Spenceri*,[1] a fossil from near Halifax; there has been some doubt as to the horizon, which is probably low down in the Upper Carboniferous. The stem has a rather small, obtusely pentagonal pith, and a very dense secondary wood, with the tracheides narrow, and the medullary rays almost always uniseriate. The leaf-traces are given off in pairs, just as in *Ginkgo*; at the angles of the pith and in contact with the woody zone there are pairs of small primary xylem-strands, corresponding to the leaf-traces. Traced downwards, the strands of each pair fuse; they are mesarch in the upper part of their course, but at a

[1] Scott, *l.c.* p. 357. *Dadoxylon* is an old name for fossil stems with wood of the Araucarian type, especially those of Palæozoic age.

lower level the centripetal wood appears to die out, as in *Poroxylon* or *Calamopitys Beinertiana*.

The interest of *Dadoxylon Spenceri* lies in its combining the wood-structure of a typical *Cordaites* with the primary xylem-strands of *Lyginodendron* or *Calamopitys* in a reduced form.

The exact relations of *Pitys* and *Dadoxylon Spenceri* cannot be determined until we know more of their structure. The characters already investigated indicate that these plants, like the Poroxyleae, belong to a plexus of forms connecting the Pteridosperms and Cycadofilices with the typically Gymnospermous family of the Cordaiteae, but standing nearer to the latter.

III. The Cordaiteae

The forms hitherto considered in this chapter appear in some respects intermediate between the Pteridosperms and the true Gymnosperms; we now pass on to a family which belongs beyond question to the latter class. The Poroxyleae and Pityeae are at present chiefly or solely known to us by their vegetative characters; we have now to deal with a group in which our evidence is drawn from all the organs of the plant—reproductive as well as vegetative. Though even here our knowledge is but limited and urgently needs to be extended, the fact remains that the family in question—that of the Cordaiteae—is one of the best known, as it is also among the most remarkable, of those which fossil botany has revealed to us.

Among the vegetable remains from the Carboniferous and Devonian strata, specimens have long been

known, such, for example, as fragments of petrified wood, which present Coniferous characters, while others, such as the impressions of large parallel-veined leaves, suggest at first sight Monocotyledons of the *Yucca* type. Associated with these remains, fossil catkin-like inflorescences (*Antholithus*) have sometimes been found, as well as a considerable variety of seeds, of the bilateral type. The piecing together, on sure evidence, of these remains, apparently so diverse, and the revelation of their structure, was essentially the work of the two French investigators, Grand'Eury and Renault,[1] though valuable contributions from other hands have not been wanting.

1. *External Characters.*—We may begin by stating the general results of the reconstruction which has been arrived at, and then go on to describe the organisation of the various organs more in detail. The Cordaiteae were tall, somewhat slender trees, with trunks rising to a great height before branching, and bearing at the top a dense crown, composed of branches of various orders, on which simple leaves of large size were produced in great abundance (Fig. 187). The stumps of the trees, with the roots attached, have often been found; the root system is said to have been rather feebly developed. The stems, in their present state, attain a diameter of a couple of feet or more, which is small in comparison with the height of the trees, for Grand'Eury finds that in various specimens the shaft alone (below the crown) reached a height of 10, 20,

[1] See especially Grand'Eury, *Flore carbonifère du Département de la Loire*, 1877, and Renault, *Structure comparée de quelques tiges de la flore carbonifère*, 1879.

or even 30 metres. It must be remembered, however,

FIG. 187.—*Dorycordaites*, sp. Restoration, showing roots, trunk, and crown, the latter composed of branches bearing large lanceolate leaves and inflorescences. The trunk is shown too short. After Grand'Eury. Modified.

that the large specimens have their wood reduced to

coal, so that the total diameter was no doubt considerably greater in the natural state, than appears from the fossil remains.

The leaves were borne in a spiral sequence, on the ultimate branches; they were simple elongated leaves, varying considerably in form in different members of the group; on these differences genera or subgenera have been founded. Thus, in the typical *Cordaites* (*Eu-Cordaites*) the leaves are spathulate, with blunt ends; they reached in some cases a length of a metre, and a width of 15 cm. To this group the forms most fully investigated belong (see Fig. 188). Then we have *Dorycordaites*, with leaves little inferior in length to those of the last group, but lanceolate and sharply pointed. Our Fig. 187 represents a restoration of a tree belonging to this subgenus. Finally there is *Poacordaites*, with grass-like leaves, reaching half a metre in length, by only a centimetre or so in breadth. The leaves of Cordaiteae, whatever their form may have been, are all characterised by parallel venation, giving them much the appearance of Monocotyledonous leaves, such as those of a *Yucca* or *Dracaena*; consequently, the earlier writers on fossil botany always placed these fossils in the class Monocotyledons. The veins are repeatedly forked, except in the narrow leaves referred to *Poacordaites*. In many instances branches have been found, bearing the leaves (cf. Fig. 188), or marked by the scars due to their fall. The scars are usually transversely elongated, and sometimes bear the prints of the vascular bundles which entered the leaf. The leaves were crowded in some forms, more remote in others, but there was always a free internodal surface

between their insertions. In some cases a lateral twig

FIG. 188.—*Cordaites lævis.* Branch (restored) bearing the large spathulate leaves, with parallel venation, and the inflorescences, each with numerous catkins. A large bud is also shown. Reduced. After Grand'Eury.

is found to be terminated by a large leaf-bud, as shown in Fig. 188.

The habit of the Cordaiteae must have been different from that of any trees with which we are now familiar. The species with comparatively short leaves may be compared with such Coniferae as *Agathis* (*e.g.* the Kauri Pine of New Zealand), or with certain forms of *Podocarpus*, and these trees may best serve to give us some idea of the appearance of the extinct family. But the longer-leaved species must have had a habit very different from anything which we are accustomed to associate with Gymnosperms at the present day.

Branches, showing the characteristic marks of *Cordaites*, have been found by Grand'Eury with structure preserved, and this important discovery enabled palæobotanists to identify a large proportion of the apparently Coniferous woods of the Palæozoic strata, named *Araucarioxylon* or *Dadoxylon*, as belonging to the Cordaiteae. The anatomical structure will be described below; here it is only necessary to say that the large size of the pith, sometimes attaining a diameter of nearly 4 inches, is characteristic of these plants, and at once distinguishes their stems from those of the Coniferae.

Casts of the pith-cavity of *Cordaites* are well-known and characteristic fossils, which used to be called *Artisia* or *Sternbergia*. They are cylindrical, or somewhat ribbed casts, sometimes very slender, but usually an inch or more, and sometimes approaching 4 inches, in diameter, and marked by numerous transverse constrictions at very short intervals, so that the whole resembles a pile of coins. Williamson, in 1851,[1] found a cast of

[1] "On the Structure and Affinities of the Plants hitherto known as *Sternbergiae*," *Mem. Manchester Lit. and Phil. Soc.* ser. ii. vol. ix. 1851.

this kind still enclosed in wood, which proved on investigation to have the structure of *Araucarioxylon*. This was one of the first steps made towards the reconstruction of these fossils, for we now know that the wood in question, resembling that of the recent Araucarias, belonged to certain members of the Cordaiteae. The peculiar appearance of the casts, as Williamson explained, is due to the discoid structure of the pith, such as is found, not only in the Walnut, and in some Jasmineae and Euphorbiaceae, but also in certain species of *Pinus*, at the present day. The pith undergoes transverse rupture in many places, so as to leave numerous diaphragms, separated by empty spaces. The constrictions on the cast in the fossil specimens, mark the position of the diaphragms (cf. Fig. 190, A).

The recognition of the true nature of *Sternbergia* has proved important, for by this means the large, rooted stumps, found in the Coal-measures of the Loire, containing *Sternbergia* casts, have been identified as belonging to Cordaiteae.

The floral organs of the Cordaiteae were known, so far as their external characters are concerned, long before their nature was recognised. These fossils, which were at first placed in the provisional genus *Antholithus*, consist of a simple or branched stalk, bearing laterally little catkin-like bodies, not often exceeding a centimetre or so in length. The male and female catkins cannot always be distinguished externally; in some forms, however, the axis of the female inflorescence appears to have borne solitary ovules, accompanied only by a few bracts.

Grand'Eury was so fortunate as to find inflorescences such as these in connection with the leaf-bearing shoots of *Cordaites*. An example (more or less restored) is shown in Fig. 188, where we see a leafy branch, bearing several fertile peduncles, each of which in its turn bears a number of catkins, probably female. The inflorescences appear to have been inserted a little above the subtending leaves, and not immediately in their axils.

We see, then, that the connection of all the organs —stems, roots, leaves, and flowers—has now been established, at least for some species of the genus *Cordaites*. The other genera or subgenera are at present less completely known. We will now go on to consider the internal organisation of the various parts, beginning with that of the stem.

2. *The Stem.*—The general type of structure of the stem of *Cordaites* was that of a Conifer, but the pith, as we have seen, was far larger than we ever find it in the Coniferae, and in its dimensions rather resembled that of a Cycad. It has already been mentioned that, in many cases (though probably not in all), the pith was discoid, as shown in Fig. 190, A. This structure was no doubt due to the fact that the more central part of the pith was not able to follow the growth of the stem in length, and consequently split across at short intervals, leaving gaps between the persistent diaphragms. At the outer edge, next the wood, the medullary tissue remained continuous.

In those specimens which were originally referred to Cordaiteae, the wood, unlike that of the Poroxyleae

and Pityeae, was wholly centrifugal in its development, the first-formed spiral elements lying on the interior margin, next the pith (Fig. 190, B, *px*); they are localised in groups, often projecting somewhat into the pith, and marking the position of the primary bundles. In stems from Shore, however, which I have recently examined, showing the discoid pith and other characters indistinguishable from those of a typical *Cordaites*, arcs of centripetal xylem are present at definite points, no doubt corresponding to the position of the leaf-traces. The structure appears to be essentially the same as in *Poroxylon*, though the number of elements in the centripetal part of the xylem-strands may be smaller. In the Cordaiteae the old "Cryptogamic" or centripetal wood appears to have been on the verge of extinction, and its presence or absence may here be of little taxonomic significance.

In Cordaiteae of the type described by Renault, the elements of the wood are radially arranged throughout, so that in transverse sections there is no distinction between primary and secondary xylem (see Fig. 189, *x*). In radial sections, however, such as that from which Fig. 190, B, was drawn, we find a marked change, from the pith outwards, in the structure of the walls of the tracheides. The narrow spiral elements of the protoxylem are succeeded by wider spiral tracheides, and these again by scalariform elements. It is not until many rows have been passed, that we come to the pitted tracheides (*bt*) which form the bulk of the wood. The transitional region between primary and secondary xylem was thus more extensive in these plants than in most of the recent Conifers.

The secondary wood has essentially the structure of that of *Araucaria*, and was hence named *Araucarioxylon* by Kraus,[1] a name which is now superfluous in cases where the connection with *Cordaites* has been established. The bordered pits, which are limited to the radial walls, are usually in two or more rows, and are

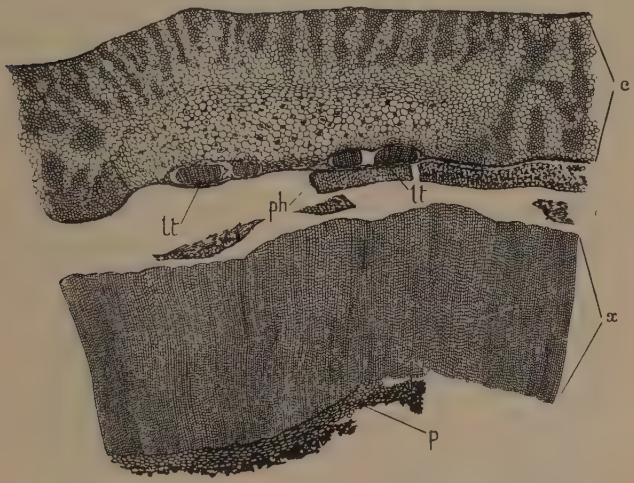

FIG. 189.—*Cordaites*, sp. Part of transverse section of a stem, from the English Coal-measures. *p*, pith ; *x*, zone of wood ; *ph*, phloëm ; *lt*, double leaf-trace, each bundle subdividing ; *c*, cortex, containing sclerenchymatous strands. × about 6. S. Coll. 306. (G. T. G.)

densely crowded in alternating series, the borders thus having a hexagonal outline (Fig. 190, B, *bt*). In good material, the pore of the pit can be recognised clearly, and has the form of an inclined elliptical slit. Certain variations in the diameter of the tracheides of successive zones were regarded by Renault as indicating periods

[1] The names *Dadoxylon*, of Endlicher, and *Araucarites*, of Göppert, are often used in the same sense as *Araucarioxylon*. *Dadoxylon* is preferable in so far as it does not suggest any affinity with the Araucarieae.

of growth, but, generally speaking, annual rings cannot be distinguished.

The medullary rays are narrow; the principal rays,

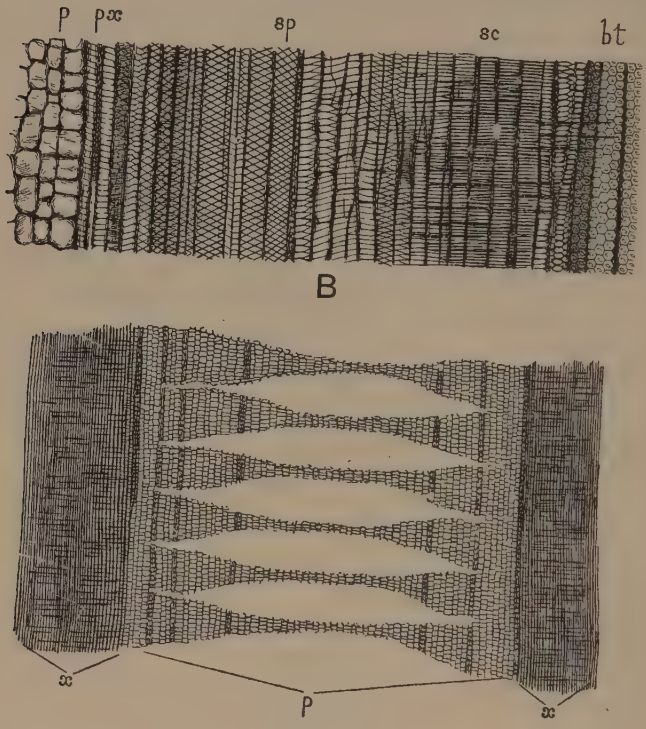

Fig. 190.—*Cordaites* (*Araucarioxylon*) *Brandlingii*. A, Radial section (somewhat restored) of middle part of stem, showing discoid pith (*p*) and wood (*x*). × about 7. B, Inner part of wood, with adjacent cells of pith, in radial section. *p*, pith-cells; *px*, narrow spiral tracheides of protoxylem; *sp*, wider spiral tracheides; *sc*, scalariform tracheides; *bt*, tracheides with bordered pits. × 95. Kidston Coll. 185 (Coal-measures of Dudley). (G. T. G.)

between the original bundles, may be as much as three cells in thickness, but the secondary rays are usually one, or at most two cells thick. The narrow rays have

been used to distinguish the wood of *Cordaites* from that of other families, such as Poroxyleae and Calamopityeae, but the distinction does not always hold good.

We see, then, that, so far as the secondary wood is concerned, the structure of *Cordaites* is indistinguishable from that of a Conifer, of the family Araucarieae.

The phloëm, when preserved, shows a radial arrangement of its elements, corresponding to that in the wood (see Fig. 189, *ph*). Sieve-tubes and phloëm-parenchyma have been distinguished, and in some forms bast-fibres are also present.

The parenchyma of the primary cortex was traversed by secretory sacs, and strengthened by many radial bands of fibres, which formed a hypodermal system, and also extended deeply into the inner cortical tissues (Fig. 189, *c*). These fibrous strands have a vertical course, and are rarely found to anastomose.

The bundles passing through the cortex on their way to the leaves are often met with in transverse sections of the stem (Fig. 189, *l.t*). In the neighbourhood of the out-going leaf-trace, in the species figured, the cortex is parenchymatous, the fibrous strands being absent (see Fig. 189). The leaf-trace was very often a double one, a point to which Williamson called attention long ago, as offering a close analogy with *Ginkgo* among recent Gymnosperms.[1] It will be remembered that we have found a double leaf-trace in *Lyginodendron*, *Ptychoxylon*, *Poroxylon*, and other cases.

[1] Williamson, "Organisation of Fossil Plants of Coal-measures," Part xii. p. 470, *Phil. Trans.* 1883, Part ii. In the section here figured (Fig. 189) each bundle of the double trace is subdivided. This represents a natural fission; in some forms of *Cordaites* it has been observed that a number of bundles entered the base of the leaf.

The character, from its frequency in Cycadofilices and the early Gymnosperms, appears to have considerable taxonomic significance—a suggestion borne out by recent work on the occurrence of the double leaf-trace in recent Gymnosperms, and in Angiospermous seedlings.[1]

The large stems of Cordaiteae are known to have formed a thick and complicated bark, but its development has not yet been satisfactorily worked out.

3. *The Root.*—Mixed with the remains of leaves and branches of *Cordaites*, silicified specimens of *roots* have also been found ; they agree so well in histological structure with the stem, that there is no reason to doubt the correctness of M. Renault's conclusion, that they belonged to the same plants, though I am not aware that roots showing structure have yet been found in actual connection with the stem. In the French specimens the roots are diarch, with a broad zone of secondary wood. The elements of the protoxylem are spiral, the rest of the primary tracheides scalariform, while the surrounding secondary zone is made up of pitted tracheides and medullary rays, and agrees in all essential respects with the wood of the stem. The root is limited on the outside by a broad zone of periderm, which, from M. Renault's description, would appear to have been derived from the external cortex. This is unusual in Gymnospermous roots, and the point seems to deserve further investigation.

Our Fig. 191 is taken from a root known as *Amyelon*

[1] Miss E. N. Thomas, "A Theory of the Double Leaf-trace, founded on Seedling-Structure," *New Phytologist*, vol. vi. 1907, p. 77.

radicans, frequent in the Lower Coal-measures of England, which in all probability belonged to some member of the Cordaiteae. All the tissues, both primary and secondary, are well preserved. In this case the roots are usually triarch—sometimes tetrarch ;

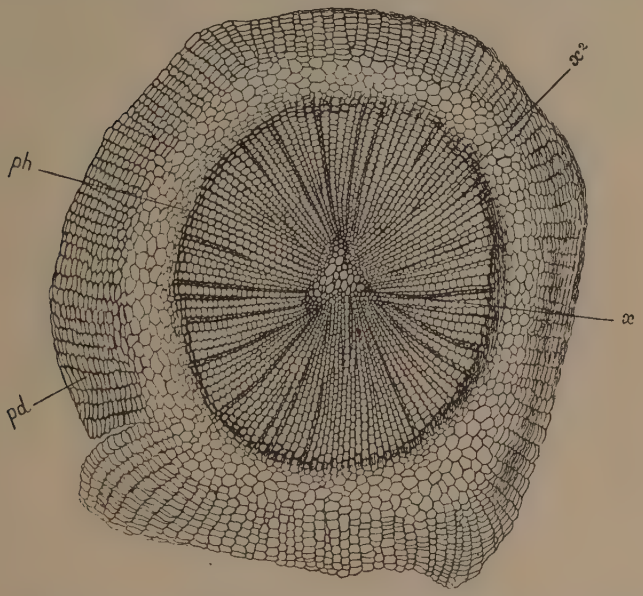

FIG. 191.—*Amyelon radicans* (probably a root of one of the Cordaiteae). *x*, triarch primary xylem ; x^2, secondary xylem ; *ph*, phloëm ; *pd*, periderm. × 23. S. Coll. 450. (G. T. G.)

in other respects there is sufficient agreement with the French specimens, to have little doubt as to the affinities of our fossil. In *Amyelon*, at any rate, the origin of the periderm was, no doubt, deep-seated, the cortex being exfoliated. The same was the case in a diarch root associated with a *Cordaites* from Shore.

4. *The Leaves.*—The leaves of *Cordaites* are fossils of frequent occurrence, especially in the Upper Coal-measures, as, for example, at Radstock in Somersetshire, and in the coal-fields of Central France, where they appear to have played an important part in the formation of coal. At St. Etienne, certain beds of coal are said to consist exclusively of dense masses of the carbonised leaves of Cordaiteae. But in addition to the carbonised remains and impressions, which are ill adapted for the investigation of structure, petrified specimens also occur. Thus, in the "black flints" of Grand Croix. silicified remains of Cordaitean leaves are packed together in layers, "like damp Beech-leaves on the ground in our forests."[1] These silicified specimens are often in a state of exquisite preservation, and rendered it possible for the French palæontologists, notably M. Renault, to work out the structure in great detail. The anatomical specimens hitherto recorded are all referable to the genus *Cordaites*, though there is often some doubt as to the particular species (as determined from impressions) to which they belonged.

Broadly speaking, the structure of the leaf of *Cordaites* resembles that of a single pinna of the leaf of a Cycad, such as *Zamia*, while there is a more general resemblance to the leaf of *Agathis*, or one of the larger-leaved Araucarias. There are, as might be expected, appreciable specific differences among the various Cordaitean leaves examined. For example, in the leaf shown in transverse section in Fig. 192, A, referred provisionally to *C. angulosostriatus*, each of the numerous parallel vascular bundles is enclosed in

[1] Solms-Laubach, *Fossil Botany*, English edition, p. 105.

a strong sheath, which abuts, above and below, on a hypodermal strand of fibres. Smaller hypodermal ribs

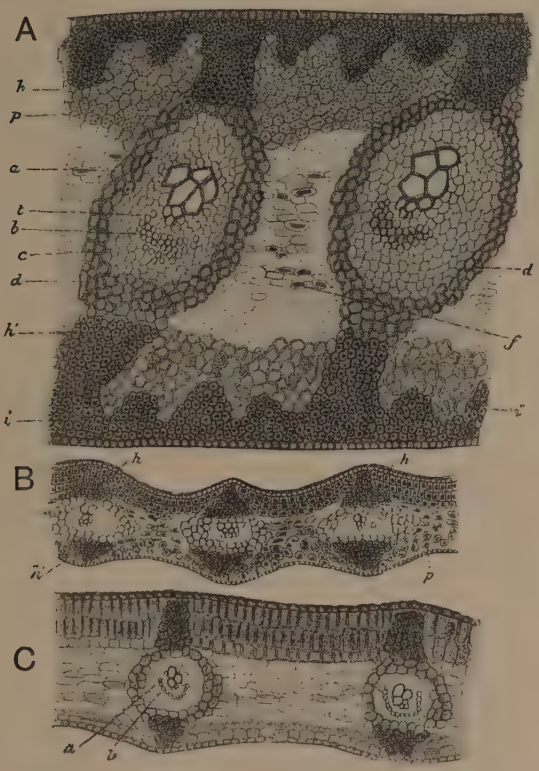

FIG. 192.—*Cordaites.* Leaves in transverse section. A. *C. angulosostriatus* (?). *h, i*, hypodermal ribs of sclerenchyma; *p*, mesophyll; *d*, bundle-sheath; *a*, centripetal xylem; *t*, protoxylem; *b*, centrifugal xylem; *c*, phloëm; *f*, tissue connecting the bundles. × 60. B. *C. rhombinervis.* Here the ribs of sclerenchyma only occur in connection with the bundles; palisade-tissue and spongy parenchyma are differentiated. × 50. C. *C. lingulatus.* Ribs as in B; palisade-tissue well marked. × 50. All after Renault.

are interposed between the vascular bundles. The bundle-sheaths are connected together laterally by transverse bridles of thickened cells, which may perhaps

be compared to the accessory transfusion-tissue which occurs in the genus *Cycas*.[1] In this species of *Cordaites*, the mesophyll shows little differentiation. The most interesting point is the structure of the bundles themselves, which agree exactly with those in the leaves of recent Cycads. The xylem is in two parts, with the spiral elements (*t*) between them. The larger portion is towards the upper surface (centripetal, *a*), and the smaller towards the lower surface (centrifugal, *b*). Below this again is the phloëm, usually ill preserved. In a word, we have in these cases (Fig. 192, A and C) the collateral, mesarch structure, characteristic of the bundles of Cycadean leaves, and already familiar to us in other fossil plants. Some other species show the same structure of the bundles, but in several the centrifugal part of the xylem is absent, as in the petioles of *Medullosa*, whereas it only dies out in the finer bundles in the case of recent Cycadean leaves.[2]

In other anatomical points there is considerable diversity of detail. The mesophyll is in some forms clearly differentiated into an upper palisade layer, and a lower lacunar portion (see Fig. 192, B and C). This is beautifully shown in a species investigated by Miss Stopes, and identified as *C. principalis*. In the same species Miss Stopes observed the very interesting fact that both the inner and outer sheaths surrounding each bundle consist of elements with bordered pits, and may

[1] A reticulate system of thick-walled tracheides, which extends from the midrib to the margin of the leaflet in this genus. See Worsdell, "On Transfusion-Tissue," *Trans. Linn. Soc.* 2nd ser. (Bot.), vol. v. 1897, p. 308.

[2] See Miss M. C. Stopes, "On the Leaf-Structure of *Cordaites*," *New Phytologist*, vol. ii. 1903, p. 91.

thus be regarded as forms of transfusion-tissue. In certain cases the hypodermal ribs are limited to the upper and lower surfaces of the bundles, not occurring between them. In one form (*C. crassus*) the leaf had a distinctly fleshy character, as if adapted to xerophytic life. Numerous stomata, of normal structure, occur in these leaves, on the epidermis of the lower surface, to which they seem to be limited. The general conclusion to which we are led is that, while the leaf, in its simple form and general structure, approaches most nearly to that of such Conifers as *Agathis*, in the details of internal organisation it agrees more closely with a single leaflet of a Cycad, thus showing a striking combination of characters, such as we have already met with in the leaf of *Poroxylon*.

5. *The Flowers.*—We now come to the most interesting point in our present subject—the floral morphology of the Cordaiteae. The general arrangement and external appearance of the inflorescences have already been described. Our knowledge of these organs has been built up by the labours of successive observers, notably Carruthers, Grand'Eury, and Renault. It is to the last-named author that our acquaintance with the intimate structure of the flowers is chiefly due, for M. Renault was so fortunate as to find silicified specimens, allowing of minute structural investigation, which were clearly of the same nature as the catkins found on the branches of the Cordaiteae. As, however, the petrified flowers could not be referred with certainty to the particular members of the family to which they belonged, the generic name *Cordaianthus*

was applied to them, and is still used, as a matter of convenience.

A. *The Male Flower*

The specimen shown in longitudinal section in Fig. 193, and known as *Cordaianthus Penjoni*, Renault, is a single male catkin,[1] corresponding to one of those which are represented in their external aspect in Fig. 188, borne laterally on the peduncles. The catkin (about a centimetre in length) consists of a rather thick axis, bearing spirally arranged bracts, between which the stamens (using the word provisionally) are inserted (Fig. 193, A). The stamens are either isolated, each in the axil of a bract, or are grouped, two or three together, around the apex of the catkin. Each stamen consists of a filament, surmounted by three, four, or more[2] long, vertical pollen-sacs. The filament is traversed by a vascular bundle, which sends a branch to the base of each pollen-sac (Fig. 193, B, *g*). Some of the sacs in M. Renault's specimens had already undergone dehiscence, by a longitudinal opening (Fig. 193, B, *e*); others are preserved intact, and are still filled with the pollen-grains (*e'*). The wall of each pollen-sac consists of a single layer of cells (Fig. 193, B). In other species (*e.g. C. Saportanus*) the stamens are limited to the apical region of the catkin, and are fewer in number; with shorter filaments.

The morphology of these male catkins of *Cordaites*

[1] The word *catkin* is used, rather than cone, to avoid any assumption of homology with the male cone of the Coniferae.

[2] M. Renault gives the number as three or four, but, as pointed out by Count Solms-Laubach, the transverse section shows five or six sacs to each stamen.

is open to various interpretations. M. Renault regards the male "flower" as consisting of a group of two or three stamens at the apex of the catkin, but as reduced to a single stamen, where the position is axillary. Count Solms-Laubach prefers to regard each

FIG. 193.—*Cordaianthus Penjoni*. A. Longitudinal section of male catkin. *a*, axis; *b*, sterile bracts; *c*, filament, bearing the pollen-sacs (*e*) at the top; *d*, junction of filament with pollen-sacs; *f*, detached pollen-sac; *v*, apex of axis, with stamens around it. × 6½. B. Stamens, more highly magnified. *g*, vascular bundle of filament, sending branches to the pollen-sacs; *e*, pollen-sac after dehiscence; *e'*, sac still full of pollen; *p*, apex of axis. Other letters as in A. × 23. Both after Renault.

of Renault's "stamens" as itself constituting a male "flower," the stalk on which the pollen-sacs are borne thus representing a pedicel, and not a filament, while the pollen-sacs are themselves the stamens. On this view there would be a certain resemblance to the male flowers of Gnetaceae. In *Gnetum*, for example,

the male flower consists of a stalk bearing two pollen-sacs, each of which is considered to represent a sessile stamen. In *Ephedra* the arrangement is similar, but the sessile stamens vary in number, according to the species, from two to eight, and each consists of two pollen-sacs. The Gnetaceae, however, are a highly modified group, as to the geological history of which we have no certain information. We must be cautious in using their morphology (which in itself is none too clear) to explain that of an ancient family like the Cordaiteae, which is known to have existed as far back as the Devonian period. If, as has recently been suggested, the flowers of the Gnetaceae are reductions from a much more complex type like that of the Bennettiteae (see Chap. XIII.) it is clear that the family can have only the most remote affinity with the Cordaiteae.[1]

M. Renault's summary of the morphological conditions in the male *Cordaianthus* certainly has the merit of simplicity. He says:—"In the midst of sterile bracts arose one or more fertile bracts, the filament of which, scarcely modified, bore at its summit three or four sacs containing the pollen."[2] On this view, the stamens would in no case be axillary structures, but would represent so many sporophylls, interspersed among sterile bracts. We might compare each stamen to that of *Ginkgo*; in the latter the pollen-sacs are usually only two in number, though stamens with three or four sacs sometimes occur, and are pendulous instead

[1] See Arber and Parkin, "Studies on the Evolution of the Angiosperms: the Relationship of the Angiosperms to the Gnetales," *Ann. of Bot.* vol. xxii. July 1908, and the papers there cited.

[2] Renault, *Tiges de la flore carbonifère*, p. 308.

of erect; these differences, however, are of trifling importance. The male catkin of *Cordaianthus* would thus chiefly differ from that of *Ginkgo*, in the presence of sterile bracts among the sporophylls, a difference comparable to the relation which we find, in a remote family, between the strobilus of a *Calamostachys* and that of a recent *Equisetum*. The data, however, are insufficient to justify any definite conclusion as to the exact morphology of the male *Cordaianthus*. It is quite clear, at any rate, that its structure is totally distinct from that of the male cone of a Cycad, and very different from that of a Conifer, or from the male inflorescence of Gnetaceae. On the whole, *Ginkgo* affords perhaps the best parallel.

The pollen-grains of *Cordaianthus* were rather large, measuring, in some examples studied by M. Renault, .09 × .05 mm., their form thus being ellipsoidal. The outer membrane had a rather rough surface; in the interior of the pollen-grain, a small group of cells (prothallus or antheridium) can often be detected (Fig. 195, C), an important observation, to which we shall return, when speaking of the phenomena of pollination.

B. *The Female Flower*

M. Renault found that the young female catkins of *Cordaites* were scarcely to be distinguished from the male by external characters, though somewhat more globular in form. In the early stages, the ovules were completely hidden by the overlapping bracts. Here also, sections of the silicified specimens have revealed the internal organisation. In a fructification, to which

the discoverer gave the name of *Cordaianthus William-*

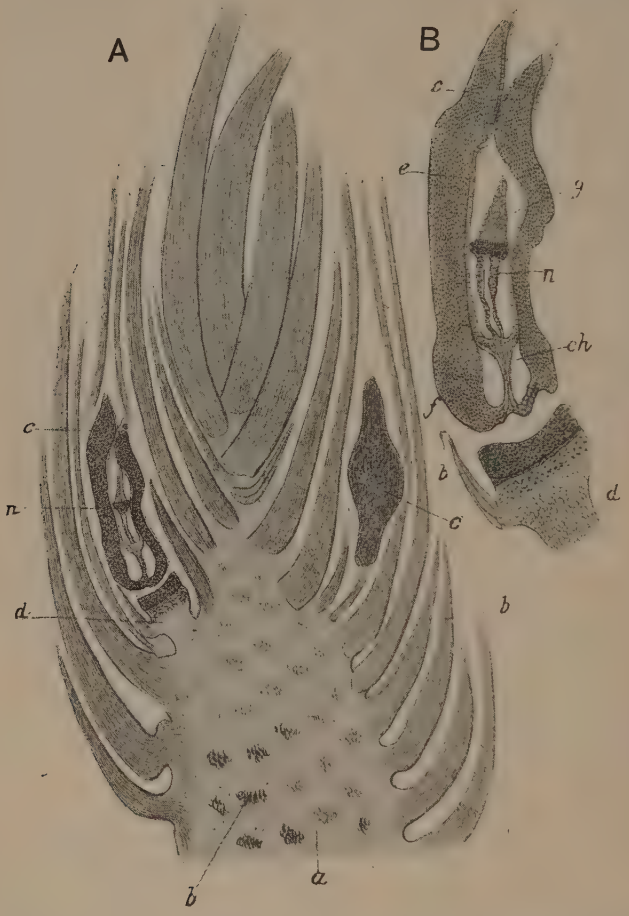

FIG. 194.—*Cordaianthus Williamsoni*. A. Somewhat tangential section of a female catkin, showing two ovules. *a*, axis; *b*, sterile bracts, and bundles running to them; *c*, ovules; *d*, axillary shoot, bearing an ovule; *n*, nucellus. × about 10. B. Ovule, more highly magnified. *d*, short axillary shoot, terminated by the ovule; *b*, bracteole; *c-f*, outer, *e*, inner integument; *ch*, chalaza; *n*, shrivelled nucellus; *g*, apex of nucellus. × about 35. After Renault.

soni (Fig. 194, A), the axis bore numerous, spirally

disposed bracts, most of which were sterile, while in the axils of some of them the ovules (*c*) were borne. Each ovule was situated at the end of a very short lateral axis (*d*), which itself bore some bracteoles; a transverse section of a similar fructification showed four ovules.

The ovule, according to M. Renault, had two integuments; the outer of the two was thick and fleshy (Fig. 194, B, *c*), while the inner (*e*) formed a delicate lining to the outer, from which it was perhaps not really distinct. At a later stage the inner layer or integument became hard and resistant, the outer remaining fleshy. In the middle was the nucellus (*g*, *n*) (somewhat shrivelled in the specimen figured), the upper part of which contained the pollen-chamber. A vascular bundle entered the chalaza, and sent out branches both into the integument and the nucellus.

Further details have been worked out in a fructification, specifically distinct, named *Cordaianthus Grand'-Euryi* by M. Renault. Here the short lateral axis, terminated by the ovule (shown detached in Fig. 195, A), bore several bracts. The outer integument is broken, and the inner has almost disappeared, leaving the nucellus nearly isolated in the middle of the ovule. In the upper part of the nucellus, we see the pollen-chamber (*c.p*), surmounted by a very curious neck, shown, on a large scale, in Fig. 195, B. Both in the pollen-chamber itself and in the canal leading to it, pollen-grains (*p*) are contained, so that this ovule, as M. Renault said, was "surprised at the very moment of pollination." The wall of the canal has a characteristic structure, for the cells in its lower part are

transversely elongated, so as to partially close the passage (Fig. 195, B, *g*). Possibly this may have been an arrangement for shutting the entrance to the pollen-chamber after pollination had been effected.

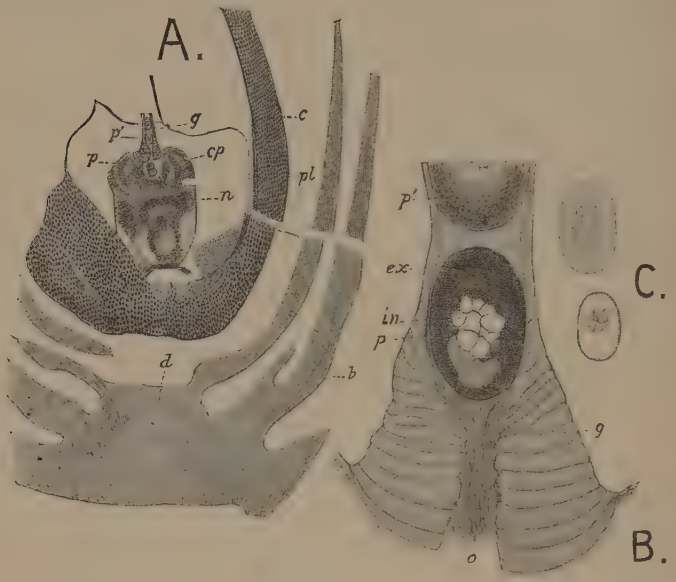

FIG. 195.—*Cordaianthus Grand'Euryi*. A. Longitudinal section of female flower, showing one ovule, just pollinated. *d*, axis; *b*, bracts; *c*, integument; *n*, nucellus; *c.p*, pollen-chamber; *g*, canal of pollen-chamber; *p*, pollen-grains in chamber, and *p'*, in canal. × 24. B. Canal of pollen-chamber enlarged. *g*, dilated cells, enclosing the canal, *o*; *p*, *p'*, two pollen-grains in the canal; *ex*, outer membrane of pollen-grain; *in*, group of prothallial or antheridial cells within the grain. × 150. C. Grains of pollen, showing internal cells; the smaller grain from an anther, the larger from the canal of an ovule. × about 100. All after Renault.

The pollen-chamber is, as we have already seen (Chap. X. p. 392, and Chap. XI. p. 453), a general feature in Palæozoic seeds. The pollen-chamber of *Trigonocarpus*, for example, among the Pteridosperms bears a rather close resemblance to that of a Cordaitean seed (see Fig. 170, p. 454). The Cycadaceae and *Ginkgo*

are the only recent plants in which this organ is known; the pollen-chamber of *Cycas* was originally discovered more than sixty years ago by our countryman Griffith, who gave excellent figures of it, which are here reproduced[1] (Figs. 196, 197). Many years later it was rediscovered independently by De Bary

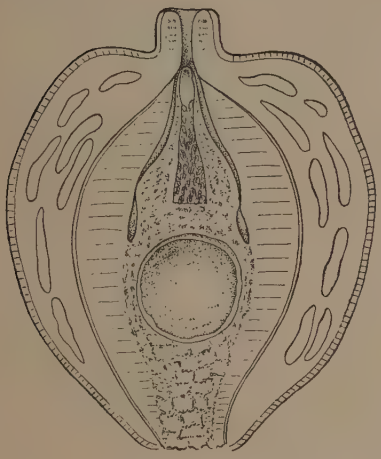

Fig. 196.—*Cycas*, sp. Longitudinal section of ovule, showing the thick double-layered integument enclosing the nucellus. The round body in the lower half of the nucellus is the embryo-sac; the flask-shaped cavity in the upper part is the pollen-chamber containing pollen-grains. From Griffith, 1852.

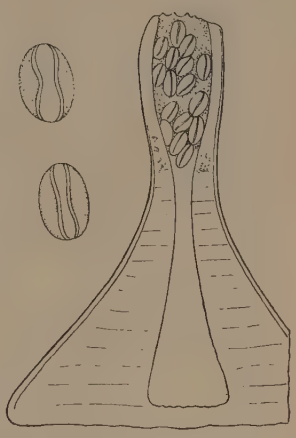

Fig. 197.—Pollen-chamber enlarged, showing pollen-grains in the canal. Two pollen-grains, further enlarged, on the left. From Griffith, 1852.

and Brongniart, both of whom were unaware of Griffith's observations.

The pollen-grains in the canal and pollen-chamber of the ovule of *Cordaites* are larger than those still contained in the anther, and their internal group of cells

[1] Griffith, *Icones Plant. Asiat.* Part iv. Pl. 377 and 378, 1852. *Notulae ad Plant. Asiat.* pp. 6-8, 1854. Both these works were posthumous; Griffith died in 1846.

is more developed (Fig. 195, C); grains, which were found lying free in the matrix, were in an intermediate condition; M. Renault drew the conclusion, that the pollen-grains continued to grow after their discharge from the anther, and more especially after their entrance into the pollen-chamber.

The cells within the pollen-grain of *Cordaites* are more numerous than in most recent Gymnosperms; in the pollen-tube of *Microcycas*, however, described by Caldwell,[1] sixteen spermatozoids are produced, while in that of *Araucaria* the number of nuclei present ranges from about twenty to forty-four.[2] In the pollen-grains of *Cordaites*, as M. Renault pointed out, the cells appear to have been all of one kind. That this structure, whether it be regarded as a prothallus or as an antheridium, should have been more developed in primæval seed-plants than is usual in those of our day, is quite what we should expect, from our knowledge of the conditions in the heterosporous Cryptogams.[3]

Pollen-grains have now been observed, in a number of instances, within the pollen-chambers of Pteridospermous and Gymnospermous seeds of the Carboniferous period. There appears to be little or no evidence at present for the formation of pollen-tubes, though the preservation is sometimes good enough for even so delicate a structure to have been detected. It is probable that such pollen-grains as those of *Cordaites* or *Stephanospermum* may have been a stage nearer the Cryptogamic microspore than those of *Cycas* or *Ginkgo*,

[1] "*Microcycas calocoma*," *Bot. Gazette*, vol. xliv. 1907, p. 118.

[2] Lopriore, "Über die Vielkernigkeit der Pollenkörner von *Araucaria Bidwillii*," *Ber. d. Deutsch. Bot. Gesellschaft.* vol. xxiii. 1905, p. 335.

[3] See the account of *Stephanospermum* above, p. 456.

that no pollen-tube was developed, but that the relatively large antheridium at once produced a number of spermatozoids, for we are probably justified in regarding the cellular body within the pollen-grain of *Cordaites* as an antheridium, rather than as a vegetative prothallus. In the absence of a pollen-tube, the spermatozoids would have needed to be more numerous, for, having a longer distance to cover by their own movements, they would presumably have reached their goal with less certainty. The pollen-tube may probably be regarded as a later adaptation, which served the purpose of economising spermatozoids, and ultimately rendered their motility unnecessary. Even in the Cycads and *Ginkgo*, where the pollen-tube serves mainly as an anchoring and food-absorbing organ, its growth ultimately brings the spermatozoids with much precision to their goal—the necks of the archegonia.[1]

As regards the morphology of the female *Cordaianthus*, there seems no reason to doubt M. Renault's view, that the ovules were borne singly, on the apex of short axillary shoots, as in *Taxus*. If we compared the female catkin with a cone, such as that of the Abietineae or Taxodieae among recent Conifers, we should be led to adopt one of the theories which interpret the seminiferous scale in those families as representing a reduced axillary shoot. Other authors have preferred the comparison with Gnetaceae, and especially with *Ephedra*, chiefly on the ground of the double integument or envelope of the ovule. It does not seem to be perfectly certain, however, that this structure in *Cordaites* was

[1] See, for example, Webber, *Spermatogenesis and Fecundation of Zamia*, U.S. Dept. of Agriculture, 1901, p. 63.

really double at its origin, and the analogy with Gnetaceae appears to be of little value. A comparison with the female fructification of *Ginkgo* has been suggested, and on general grounds would seem justified, but the homologies of the parts have not been clearly determined. However this may be, it appears evident that, in the case of the female flower, the indications of affinity point towards Coniferae or Ginkgoaceae, rather than towards Cycadaceae, to which, so far as the floral morphology is concerned, the Cordaiteae seem to bear little resemblance. We must, however, remember that our living Cycads only represent one or two special surviving groups of a Class once infinitely more extensive and varied. The possibility of a comparison between the floral structure of the Cordaiteae and that of certain Mesozoic Cycadophyta (the Bennettiteae) has been maintained by some botanists, but no longer appears tenable (see Chap. XIII.).

6. *The Seeds.*—In some cases seeds, in a more or less ripe state, have been found attached to the inflorescence, and in connection with the leafy twigs of Cordaiteae. These seeds sometimes appear to have been solitary, a single seed representing the female catkin as found in the younger specimens of such fructifications as *Cordaianthus Williamsoni*. This may indicate a real morphological difference, like that between *Taxus* or even Ginkgoaceae and the Coniferae with true cones, but it may be equally well explained if we suppose that only one ovule in each catkin developed into a ripe seed. In some specimens, as in *Cordaianthus anomalus*, Carruthers, each seed

was seated on a long slender stalk or peduncle;[1] this may have been developed during the ripening of the seed. Our knowledge of the comparative morphology of the Cordaitcae has unfortunately made little progress in recent years, owing to the want of adequate material.

In certain cases, characteristic heart-shaped seeds have been found in connection with the inflorescences of *Cordaites*. This has rendered it possible to identify, with great probability, a certain number of the isolated seeds, as belonging to this family. Such direct evidence is very necessary, for, as we have already seen (Chaps. X. and XI.), a large number of the Palæozoic seeds belonged to Pteridospermeae, and, where they were of the platyspermic type, may be extremely difficult to distinguish from those of Cordaiteae. It is also probable that the seeds of primitive Coniferae and Cycadophyta (both of which groups already existed, at least in the later Palæozoic times) may be represented among the detached seeds. We will first describe that type of seed which is known, from the evidence of attached specimens, to have been produced by the Cordaiteae, and was therefore named *Cordaicarpus* by M. Renault.[2]

These seeds are heart-shaped at the base, and somewhat flattened, being of the platyspermic type. The testa is double, the outer envelope, or sarcotesta, having been soft and fleshy during life, while the inner layer,

[1] Carruthers, "Notes on some Fossil Plants," *Geol. Mag.* vol. ix. 1872.

[2] These seeds were originally named *Cardiocarpus* by Brongniart, a name used by Carruthers and Williamson in the form *Cardiocarpon*. As pointed out in Vol. I. Chapter VI. (p. 194), certain "seeds" referred by Williamson to *Cardiocarpon* really belonged to Lycopods and are now named *Lepidocarpon*.

or sclerotesta, was hard and lignified. M. Renault regarded the two layers of the testa as having been derived from two integuments, a view which he believed to be supported by the structure of the ovule, as above described. There is, in fact, the same doubt here as in the case of recent Cycadaceous seeds, in which some botanists regard the double testa as representing two integuments, while others consider that a single integument has undergone differentiation into distinct layers.

The vascular bundle which enters the chalaza gives off branches, both into the testa and into the nucellus; the former traverse the inner part of the sarcotesta, a single or double bundle running up on each side of the seed, just outside the lateral edges of the sclerotesta (cf. *Rhabdocarpus*, Fig. 185), while the latter enter the nucellus and apply themselves to the membrane of the embryo-sac. At its micropylar end, the nucellus, which was probably free from the integument, contains a pollen-chamber, provided with a neck, which projects into the micropyle. Apart from its bilateral symmetry, the seed agrees very nearly in structure with the *Trigonocarpus* type, described on p. 452. In certain species of *Cordaicarpus* the archegonia have been found. They occur in the usual position, at the upper end of the endosperm, and two of them are shown in a longitudinal section of the seed.

Our illustration, Fig. 198, is from a seed which M. Renault separated generically from *Cordaicarpus*, on account of the distribution of the vascular bundles. In *Cycadinocarpus*, as the new genus is named, the inner vascular system follows the endotesta, and does

not enter the nucellus, a course which resembles that in the seeds of recent Cycads, as interpreted by many observers. In other respects the seed agrees with *Cordaicarpus*. Two archegonia (*ar*), spherical in form, are clearly shown; between them, the endosperm has an upward prolongation, which is interesting, as it exactly corresponds to the structure found in *Ginkgo* at the present day, and compared by Hirase to a

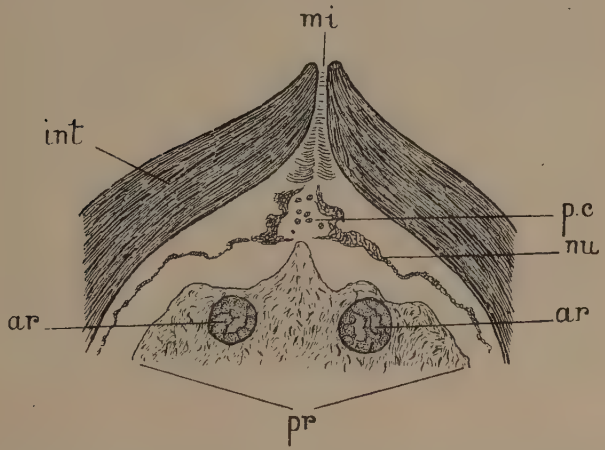

FIG. 198.—*Cycadinocarpus augustodunensis*. Upper part of seed, in longitudinal section, *int*, integument; *mi*, micropyle; *nu*, remains of nucellus; *p.c*, pollen-chamber, containing pollen-grains; the chamber has a long neck or canal, extending up into the micropyle; *pr*, endosperm; *ar*, archegonia. Magnified. After Renault.

tent-pole, supporting the nucellar membrane, which represents the tent. The pollen-chamber (*pc.*), with its long neck rising up into the micropyle (*mi*; cf. Figs. 196 and 197), contains pollen-grains. Only the sclerotesta (*int*) of the seed is shown in the figure.

Although so many Pteridospermous and Gymnospermous seeds have been discovered in the Carboniferous formation, and often in a wonderful state of

preservation, no embryo has, as yet, been found in any of them. The possible explanation of this fact has been discussed in connection with the seed of *Lyginodendron* (see Chap. X. p. 393).

The investigation of the Palæozoic seeds, which was allowed to rest for some time after the classical researches of Brongniart, Renault, and Williamson, is now again being actively pursued, having been greatly stimulated by the discovery of the seeds of the Pteridosperms.

7. *Affinities.*—We have now completed our sketch of the principal characters of the Cordaiteae, and may briefly sum up the conclusions to which we are led.

In their vegetative characters, the Cordaiteae hold the balance very evenly between Cycads and Conifers, while at the same time showing much that is peculiar to themselves. The structure of stem and root is, on the whole, very near that of the Coniferae; the secondary wood especially would by itself rouse no suspicions that we had anything but an Araucarian Conifer before us. The large size of the pith in the stem, however, is unlike anything known in Coniferae, and rather suggestive of a Cycad, though in its peculiar discoid structure the pith of some Cordaiteae is quite different from that of Cycads.

The double leaf-trace is a striking point of agreement with *Ginkgo* on the one hand, and with certain of the Pteridosperms on the other; Poroxyleae form a connecting link with the latter in this respect.

The wood of the stem was wholly centrifugal in development, in many of the specimens investigated

belonging to undoubted Cordaiteae ; but this distinction is no longer absolute, for, as we have seen, there are stems, apparently of true Cordaiteae, in which some centripetal wood is present, as it is in the Poroxyleae and Pityeae. In fact, on our present knowledge it is impossible to draw any sharp distinction between these three families, and we have therefore grouped them under the common name Cordaitales. If the seeds of *Poroxylon* are represented, as M. Grand'Eury believes, by *Rhabdocarpus*, the very close affinity of this family to true Cordaiteae is further confirmed.

The leaves, in their general form and venation, recall those of such Coniferae as *Agathis*, though often greatly exceeding those of any known Conifer in size.[1] In internal structure the leaves agree almost exactly with the single pinnae of the leaf in Cycads.

In general habit, the lofty stem, with well-marked internodes, departs altogether from the ordinary Cycadean type, and much more resembles that of a Conifer, but, in many species, at any rate, the crown, with its abundance of huge simple leaves, must have presented an appearance totally unlike anything in either of the recent families.

It is to the reproductive organs—the male and female fructifications and the seeds—that we naturally attach the chief importance in considering the affinities of the Order. It is just in these organs, however, that we find the most remarkable combination of characters, both such as are common to various other families and such as are altogether peculiar to the

[1] In *Agathis macrophylla*, from the Queen Charlotte Islands, the leaves attain a length of 17 cm., and a breadth of 5 cm. Seward and Ford, "The Araucarieae," *Phil. Trans. Royal Soc.* B, vol. 198, 1906, p. 315.

fossil group. The staminiferous flowers (however we may interpret them) are very different from anything known to us, either in the Cycadaceae or the true Coniferae. A comparison, though in either case a remote one, is possible with the Gnetaceae (*Gnetum* or *Ephedra*), on the one hand, or with *Ginkgo*, on the other. On the former alternative, we should have to regard the stalked tuft of pollen-sacs as representing an axis, bearing sessile anthers; on the latter, we should interpret it as a single sporophyll, with terminal microsporangia. The latter view is the simpler, and the analogy with *Ginkgo*, in many respects a primitive type, is more valuable than that with the highly specialised Gnetaceae. On any view, however, the organisation of the male flower of Cordaiteae is quite peculiar, and unlike that in other Gymnosperms, and even if it stood alone, would serve to mark them as a distinct Order.

The female strobilus, like the male, is as remote as possible from that of the Cycads, but agrees well enough with the cone of the Coniferae, if we adopt the view that in the latter the ovule is borne on an axillary shoot, more or less modified. This, in fact, seems, provisionally, quite a tenable view, for on this supposition we should have the ancient Cordaiteae showing, in its simplest form, an arrangement which became much modified and disguised in the more recent Order, Coniferae.[1] At the same time it must be admitted that the true relation of the Cordaiteae to the Coniferae is still an open question (Chap. XIV.). The

[1] For a summary of the various views as to the morphology of the female cone in Coniferae, see Worsdell, *Annals of Botany*, March 1900.

affinity with Ginkgoaceae, which in many respects also hold an intermediate position between Cycadophyta and Coniferae, appears the strongest from every point of view.

The comparison of the female inflorescence with that of the Gnetaceae seems to rest on a very weak basis. It is not proved beyond doubt that the ovule of Cordaiteae had two integuments, still less is there any indication that the two were of a different morphological nature, as appears to be the case in Gnetaceae. It is probable that the affinities of the Gnetaceae may lie in quite a different direction, namely, in that of the Mesozoic Bennettiteae (see Chap. XIII.).

The structure of the seeds which are known to have belonged to Cordaiteae, is altogether Cycadean, and, as we have seen, even minute details, such as the form of the pollen-chamber, can be exactly paralleled among recent Cycads. These facts, together with the foliar structure, appear to prove conclusively a real affinity between the two families, though in other respects they diverged widely from one another. But just in the points where there is a strong agreement with Cycadaceae (with Bennettiteae the relation, as regards the seed-structure, is much less close) the Pteridosperms are likewise approached. The anatomical characters, together with the seed-characters and those of the multicellular pollen-grain, show such manifest correspondence that there can scarcely be a doubt that Cordaiteae sprang from the same stock with Pteridosperms, though at a very remote period. The characters which they share with the Cycadophyta

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may be due to their common origin rather than to a direct connection in later periods.

Returning for a moment to the anatomical characters, it may be pointed out that the general structure of the leaf in Cordaiteae agrees so closely in essential points with that of *Poroxylon*, that we can scarcely doubt that the two groups were nearly allied. *Poroxylon* retained centripetal wood in the stem, a primitive character which some of the Cordaiteae had lost. The Poroxyleae appear thus to combine the characters of Lyginodendreae or Calamopityeae with those of Cordaiteae, though their horizon is too late for us to regard this family as an actual link with the Pteridosperms. The Pityeae belong to the earliest Carboniferous times, but, to judge from the few characters available for investigation, were already far advanced on the Cordaitean line of descent.

The affinities of the Cordaiteae and of the Cordaitales generally are, as we have seen, extraordinarily complex, and cannot be cleared up until our data are much more extensive than at present. The great step which has been made in the last few years is the full confirmation of the affinity between Cordaitales and the Pteridosperms, which the discovery of the seeds of the latter class has afforded. The relations to Cycadophyta, Ginkgoaceae, and Coniferae have long been recognised, and thus a strong presumption is established that the whole of the Gymnosperms sprang originally from the same ancient stock of Fern-like plants (see Chap. XIV.).

CHAPTER XIII

THE MESOZOIC GYMNOSPERMS

I. CYCADOPHYTA

OUR studies have so far been almost entirely limited to plants of Palæozoic age; in order to carry out our plan of directing attention to discoveries of fundamental botanical importance, we have now to give an account of the Mesozoic Cycadophyta, a group among which some of the greatest triumphs of Palæobotany have been won.

From the Trias onwards to the Lower Cretaceous, the Mesozoic vegetation maintained, on the whole, a very uniform character, widely different from that of the preceding Palæozoic period. Throughout the earlier Mesozoic ages true Ferns were abundant, more so, no doubt, than in the preceding period; Conifers, often much resembling recent types, had become a dominant group, and the family now represented solely by the Maidenhair tree (*Ginkgo*) was of considerable importance. The most striking feature of the vegetation, however, in all parts of the world, was the abundance of plants belonging to the same great class with the recent Cycadaceae, now so

limited a group. The Cycadophyta, in fact, were as characteristic of Mesozoic vegetation as are the Dicotyledons of our present Flora. Among the commonest remains are leaves, which in many cases closely simulate those of existing Cycadaceous genera, and have hence received the names *Zamites*, *Dioonites*, and *Cycadites*. These generic resemblances, however, are usually deceptive; the *Zamites* and *Dioonites* leaves are now known to have belonged to plants which had only a somewhat distant affinity with the Order Cycadaceae, while in certain leaves once referred to *Cycadites*, or even to *Cycas* itself, the similarity to those of the recent genus has proved to be illusory (see below, p. 595). In other leaf-genera, again, such as *Otozamites* and *Anomozamites*, the foliage, while of a Cycadean type, differs evidently from that of any of the existing genera.[1]

In addition to the leaves, fossil trunks, which present the external characters of Cycadean stems, are of common occurrence in the older Secondary rocks, as, for instance, in the Wealden of Sussex and in the well-known "dirt-bed" of the Lower Purbeck strata in the Isle of Portland, and at other places along the Dorsetshire coast. The stems are usually short, though they may appear shorter than they actually were, owing to pressure of the superincumbent strata. The surface is usually covered by the closely-set bases of the leaves; the upper end of the stem is commonly hollowed out, owing to the decay of the growing apex. "Fossil crows' nests" is the name by

[1] Numerous figures of the leaves of Mesozoic Cycadophyta will be found in Seward's *Catalogue of the Mesozoic Plants in the Department of Geology, British Museum*, Parts ii.-iv. 1895-1904.

which such specimens are known to the Portland quarrymen. In certain trunks from the Sussex Wealden, named *Bucklandia* by Mr. Carruthers, an alternation of the scars of foliage and scale leaves has been traced, such as is found in *Cycas* at the present day. In some cases the stems attained a more considerable height, as in the *Cycadeoidea gigantea* of Seward, a fine specimen of which, almost 4 feet high, with a girth of $3\frac{1}{2}$ feet, was found some years ago in the Isle of Portland, and is now set up in the Geological Department of the British Museum.[1] In favourable cases the Cycad-like stems are completely silicified, and their structure preserved with wonderful perfection. A number of important specimens of this nature, referred to many species, have been found in our own country, France, Italy, and other parts of Europe, but the United States of America are far richer than any other country in such material. No less than sixty species of silicified trunks of Cycadophyta have already been described from the Mesozoic of North America, ranging in age from the Upper Triassic to the Lower Cretaceous. In the Eastern States the Potomac beds of Maryland (approximately of Wealden age) have yielded seven species, but the richest localities are in the West, on the Rim of the Black Hills of Dakota and the Freezeout Hills of Wyoming; from the Upper Jurassic and Lower Cretaceous beds of these districts forty-nine species have been obtained. The specimens are very numerous; thus the twenty-nine species from the Black Hills of

[1] Seward, "On *Cycadeoidea gigantea*, a New Cycadean Stem from the Purbeck Beds of Portland," *Quarterly Journal of the Geol. Soc.* vol. liii. 1897.

South Dakota are represented by nearly 1000, more or less complete trunks.[1] The Cycadophyta of the American Mesozoic rival in palæontological value the

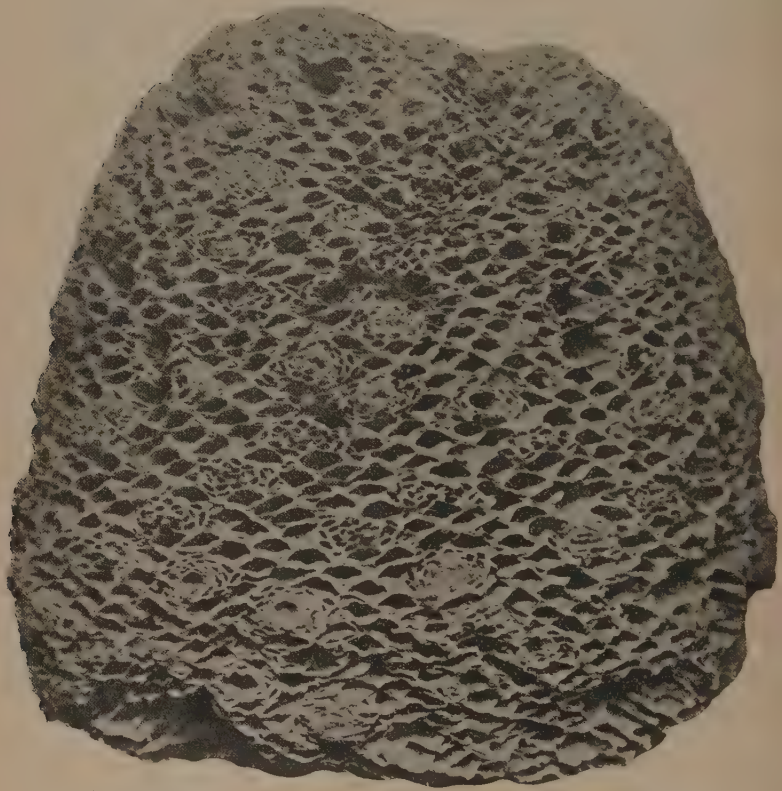

FIG. 199.—*Cycadeoidea marylandica.*—The earliest described American fossil Cycad. From an original daguerrotype. Nearly thirty young fruits are marked in the present view by the groups of bract-scars interpolated between the old leaf-bases. About ¼ natural size. From Wieland.

gigantic Saurian animals, with the remains of which they are often associated. Fig. 199 represents the

[1] See Wieland, *American Fossil Cycads*, Carnegie Institution, Washington, 1906, and the systematic works by Lester Ward, there cited.

trunk of *Cycadeoidea marylandica*, the first American Cycad to be discovered; it was found about the year 1860, between Baltimore and Washington, by the geologist Philip Tyson. Many years elapsed before any further discoveries were made; it was not till 1893 that additional specimens came to light in Maryland and that the rich deposits of the Black Hills of Dakota began to be explored.

The vast majority of the Mesozoic Cycadophyta at present investigated differ essentially from the existing Order Cycadaceae, and have been grouped under the family name Bennettiteae or Cycadeoideae.

1. *Bennettiteae.*—In a great number of cases, fructifications have been found in association, or, more often, in actual connection, with the stems of Cycadophyta, and it is only in the rarest instances that these fructifications have proved to be of the Cycadean type, as known to us from its recent representatives. In an overwhelming majority of the fructifications belonging to the Mesozoic Cycadophyta (using that form of name, as suggested by Professor Nathorst, to indicate a group enormously wider than our recent Cycadaceae), the structure of the organs of reproduction is found to have been totally different from anything known in the recent Order, and of a far more highly differentiated type. The main purpose of the present chapter is to give some account of these plants, which formed the dominant group of Cycadophyta in the Mesozoic period.

The family in question is that of the Bennettitcae, so named from the type-genus *Bennettites*, founded by Mr.

Carruthers in 1868, for several species, ranging from the Middle Oolite to the Lower Greensand. The characters of the genus were thus given by the author in his classic memoir:—"*Trunk* ovoid, in transverse section elliptical, covered with the somewhat long permanent bases of the petioles. *Medulla* entirely cellular, with numerous gum-canals. *Wood* consisting of a thin interrupted cylinder of striated tissue, everywhere penetrated by medullary rays. *Fruits* borne on secondary axes, not protruding beyond the bases of the petioles."[1]

The elliptical transverse section of the stem has not proved to be valid as a generic or even a specific character, but on the whole the short description just quoted still holds good. The American palæobotanists use Buckland's generic name *Cycadeoidea* in preference to *Bennettites*.

The following account is based in the first instance on the observations of Carruthers (who laid the foundation of our knowledge of the group), Solms-Laubach, Lignier, and others, confirmed, as regards the fructification of *Bennettites Gibsonianus*, by a study of the original preparations. The still more important results obtained from the investigation of the American material by Dr. Wieland have in some respects profoundly modified our conception of the group, and will be considered in due course.

In external aspect, the stems of the Bennettiteae presented the same general appearance as those of the recent Cycads in which the stem remains clothed in an

[1] Carruthers, "On Fossil Cycadean Stems from the Secondary Rocks of Britain," *Trans. Linnean Soc.* vol. xxvi. 1870.

armour of persistent leaf-bases (see Fig. 200, B). The dimensions were also of the same order. The stem of

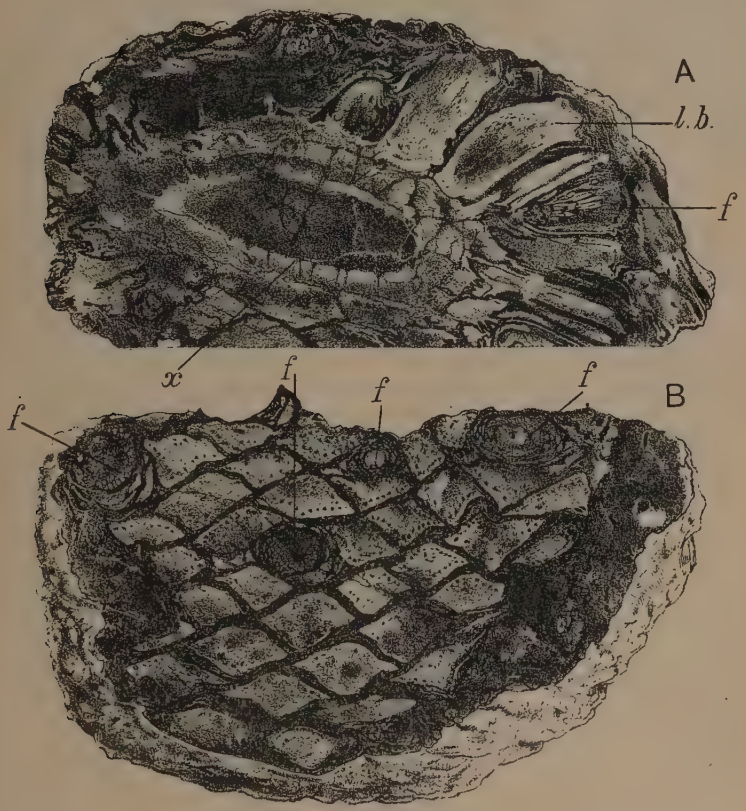

Fig. 200.—*Bennettites Gibsonianus*. A. Stem in tranverse section, showing the ring of wood, *x*, surrounding the large pith, the leaf-bases, *l.b.*, completely covering the surface, and a fructification, *f*, seen in longitudinal section, between the leaf-bases. B. Stem in tangential section, through the armour of leaf-bases, the vascular bundles in which are shown. Several fructifications, *f*, are seen, in transverse section. Both reduced. From the *Linnean Soc. Trans.* After Carruthers

B. Gibsonianus, shown in Fig. 200, from Mr. Carruthers' paper, attained a maximum diameter of 11 inches; a

considerable part of this diameter was made up of the persistent leaf-bases, as shown in the figure. The American species *Cycadeoidea marylandica*, represented in Fig. 199, was of larger dimensions, and may serve as a typical example of the external characters of the family. The great feature in which these stems differ, even in outward aspect, from those of any recent Cycads, is the presence of numerous short lateral branches, resembling large buds, which are wedged in here and there between the bases of the leaves (Figs. 199, 200, *f*). These lateral appendages are the fructifications, one of which is shown in Fig. 200, A, in longitudinal section, inserted by a short stalk on the stem, and lying horizontally between the bases of the leaves. It is probable that the position of the fructifications was axillary; in any case they were lateral branches, and cannot have been terminal on the main axis, thus differing in position from the cones of living Cycads. Hence, the fertile stem of *Bennettites* appears to have had a monopodial, and not, as in the recent Order, a sympodial construction.

The main features in the anatomy of the stem were worked out by Carruthers, whose conclusions have been confirmed by the work of later investigators. The structure is shown with special clearness in *Bennettites Saxbyanus*, a species from the Wealden beds of Brook Point, in the Isle of Wight (see Fig. 201). The large pith is surrounded by a ring of wood and bast, of no great thickness, built up as in normal Gymnospermous stems, of anastomosing vascular bundles with collateral structure. The histological details of both wood and bast (which have more recently been minutely studied

by Count Solms-Laubach in an Italian species, and by Dr. Wieland in the American material) agree precisely with the corresponding structures in a recent Cycad.

It is only when we come to the course of the bundles passing out to the leaves, that important differences

FIG. 201.—*Bennettites Saxbyanus.*—Transverse section of stem. *p*, pith; *x*, wood, *ph.*, phloëm, together constituting a ring of collateral bundles; *l.t.*, leaf-trace bundles, passing out through the cortex, and subdividing repeatedly; *l.b.*, bases of leaves, which clothe the stem. Reduced. From the *Linnean Soc. Trans.* After Carruthers.

show themselves. In recent Cycads, as is well known to the botanical student, the course of the leaf-traces is peculiar and characteristic. To supply each leaf, two bundles leave the stele; they start near together, and, curving in opposite directions, pass nearly half way round the stem, thus entering the leaf-base on the opposite side from their starting-points. They then

subdivide, to form the numerous bundles of the petiole. In their course through the cortex, the outgoing bundles are connected by cross-branches with one another, as well as with other leaf-traces, and with the bundles of the primary ring.[1]

In *Bennettites* the arrangement is a far simpler one. A single bundle leaves the ring, starting from the lower angle of one of the meshes, which (as shown in tangential section) are occupied by the primary medullary rays. As the leaf-trace passes out through the cortex, it assumes a horse-shoe form, with the concave side inwards. It then breaks up by successive subdivisions into a number of smaller bundles, which enter the base of the leaf (see Fig. 201, *l.t.*).

In the petiole, the vascular bundles arrange themselves in an almost closed curve, slightly open and involuted towards the upper surface, as is well shown in tangential sections passing through the armour of leaf-bases see (Fig. 200, B).

In some Bennettiteae, as, for example, in the species *B. Peachianus*, from the Middle Oolite of Sutherland, the pith contains several isolated rings of differentiated tissue, which at first sight suggest medullary vascular strands, and were at one time erroneously compared with the central steles or "star-rings" of the Permian Medulloseae.[2] More recent observations leave no doubt that the medullary rings occurring in *Bennettites*

[1] See De Bary, *Comparative Anatomy of Phanerogams and Ferns*, English edition, p. 608.

[2] See above, Chapter XI. p. 441. The statement, to this effect, in Solms-Laubach's *Fossil Botany*, p. 98, was corrected by him in his joint work with Capellini, on the trunks of Italian Bennettiteae, *Mem. R. Accad. Sci. Bologna*, vol. ii. 1891.

have nothing to do with the vascular system, and consist merely of bands of internal periderm, an abnormal condition which is often met with in the stems of recent Cycads.

We see, then, that the structure of the Bennettiteae, so far as it is at present known, was a simple monostelic one, resembling in its main features that of the less complex Cycads now living, but differing from any existing Cycads in the simpler course of the bundles supplying the leaves. In this latter point, the Bennettitean stem has been compared by Solms-Laubach with the peduncle of recent Cycads, an organ which in other points also appears to show a more primitive anatomy than that of the vegetative stem.[1]

In *Cycadeoidea Jenneyana*, one of the Dakota trunks, there is some evidence for the presence of numerous successive zones of wood and bast, as in the recent *Cycas* and *Macrozamia*, but the point is not yet settled.[2]

In *B. Gibsonianus*, the vascular bundles of the leaf-bases are beautifully preserved, and show essentially the same structure as the foliar bundles of the recent Cycadaceae. They are of the collateral mesarch type, whereas those of the stem are endarch; the centripetal wood forms a mass of large elements, with a band of the radially arranged tracheae of the centrifugal wood on the outside. The same structure is found in various American species, but in *Cycadeoidea micromyela*, a French species probably of Liassic age, centripetal wood appears to be entirely absent.[3] The detailed

[1] See Chapter X. p. 366.

[2] Wieland, *American Fossil Cycads*, p. 79.

[3] Lignier, "Végétaux foss. de Normandie, III. *Cycadeoidea micromyela*," *Mem. Soc. Linn. de Normandie*, t. xx. 1901.

structure of the xylem in the bundles of Bennettiteae still needs further investigation. Beyond the wood is the phloëm, often fairly preserved, and the outer edge of the bundle is occupied by a group of bast-fibres.

The parenchymatous tissue, both of the stem and leaf-bases, abounds in large gum-canals, the contents of which have often become fossilised. These organs closely resemble the similar secretory passages in recent Cycads.

Between the leaf-bases, and around the fructifications and their bracts, the spaces are densely packed with multicellular hairs, very different from anything known in Cycadaceae, but closely resembling the ramenta of Ferns. The hairs are scale-like structures, one cell thick near the margin, but reaching a thickness of from two to five cells in their middle part (see Fig. 203, B). The cells of which they are composed attain a great length in the longitudinal direction of the ramentum. The ramenta are borne both on the leaf-bases and on the bracts, which, as we shall see, envelop the fructification. The Fern-like character presented by the ramenta is a surprising feature in a genus so far advanced in Phanerogamic organisation as *Bennettites*.

We now come to the consideration of the fructifications themselves, and in approaching this subject we must divest our minds of all preconceptions drawn from a knowledge of existing Cycadean cones. The reproductive organs of the Bennettiteae are wholly different in organisation, both from the cones which characterise the majority of recent Cycadaceae, and from the rosette

of leaf-like carpels which forms the female flower in the genus *Cycas*.

The following description of the fructification is based, in the first instance, on the species *Bennettites Gibsonianus*[1] of Carruthers. In this species only the female organs are known, but, as we shall see later, the investigation of the American material has proved that in most cases, and possibly in all, the fructification was hermaphrodite. We have already learnt that each fructification is a lateral appendage, seated by a short stalk on the main stem. The whole fruit is somewhat pear-shaped, and about 5 centim. in extreme length. Although fully ripe in the specimens investigated, as shown by the condition of the seeds, the fruit is completely enclosed in imbricated bracts, which spring from the stalk, and close in over the apex (see diagram, Fig. 203, A, and Fig. 202).

The stalk is expanded into a hemispherical receptacle, on which all the organs of the fruit are inserted. From the convex surface of the receptacle spring a great number of slender pedicels, which pass vertically upwards, or diverge slightly towards the curved surface of the fruit. Each of these pedicels bears at its end a single erect seed, with the micropyle directed outwards (see Fig. 202, and diagram, Fig. 203, A). The seeds are so placed that their micropyles meet the surface of the fruit approximately at a right angle.

The spaces between the pedicels are packed with

[1] The original specimen of this magnificent fossil was found by Mr. T. F. Gibson in 1856 or 1857 in the Lower Greensand at Luccomb Chine, in the Isle of Wight. Part of the specimen is now at Kew, and part at the British Museum (Natural History Department). A second specimen was afterwards discovered by Dr. Leeson, of Bonchurch, Isle of Wight.

sterile appendages, which may be called the interseminal scales. Towards the periphery of the fruit, in its lower portion, the sterile organs are more numerous

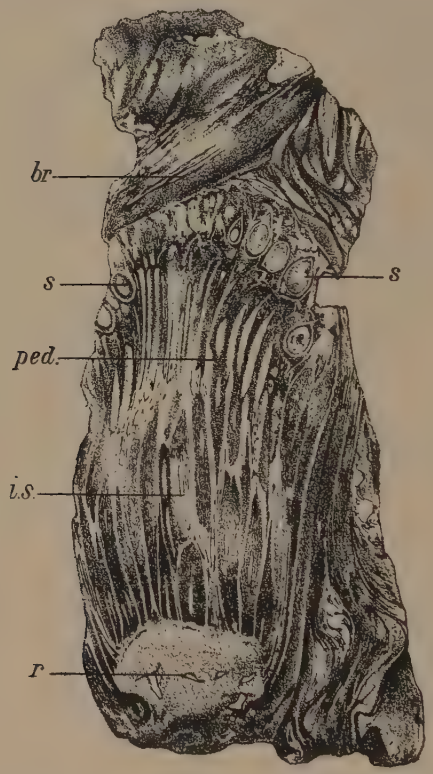

FIG. 202.—*Bennettites Gibsonianus*. Longitudinal section of a fructification. *r*, receptacle; *br*, bracts, enclosing the fruit; *s*, seeds, each borne at the summit of a long pedicel, *ped.*; *i.s.*, interseminal scales. × about 2. From *Linnean Soc. Trans.* After Carruthers.

than the pedicels, and around the base of the receptacle the former are present alone (Fig. 203, A).

All the organs of the fruit are closely packed together, and at its periphery (*i.e.* immediately within

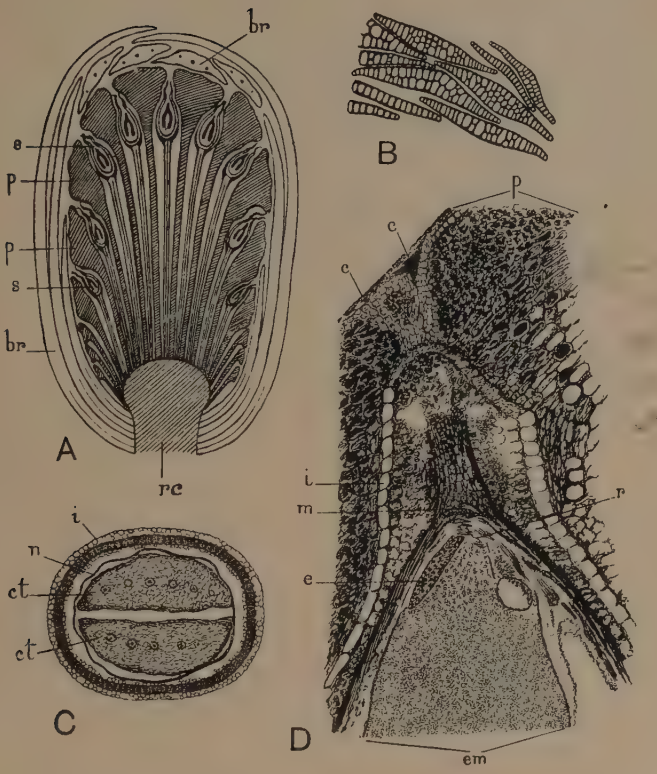

FIG. 203.—*Bennettites Gibsonianus*. A. Diagram of the fruit, in radial section. *rc*, receptacle; *br*, bracts, which overlap at the top of the fruit; *s*, seeds, each borne on a long pedicel, springing from the receptacle; in each seed the dicotyledonous embryo is indicated; *p*, dilated ends of the interseminal scales, which, in nature, are more numerous and become confluent, forming the pericarp. Modified, after Solms-Laubach and Potonié. B. Ramenta, in transverse section. × about 15. C. Transverse section of a seed. *i*, the double-layered testa; *n*, membrane representing the nucellus; *ct*, the two cotyledons of the embryo; in each cotyledon the procambial vascular bundles are visible. × about 12. S. Coll. 350. D. Somewhat oblique longitudinal section through the micropyle of a seed. *em*, radicular end of embryo; *r*, apex of radicle; *e*, remains of endosperm (?); *m*, micropyle, obliquely cut by the plane of section; *i*, outer layer of testa; *p*, part of pericarp; *c*, *c*, crevices in pericarp, corresponding to the limits of its constituent interseminal scales. × 20. S. Coll. 357. The original figures B, C, and D, as well as Figs. 204 and 205, are from sections cut for Count Solms from the type-specimen, and now in my collection. (G. T. G.)

the enveloping bracts) the tissue appears to be actually continuous, forming, as it were, a closed pericarp, perforated only by the micropyles of the seeds (see Fig. 203, A and D, *p*). The pericarp is formed by the cohesion of the interseminal scales. These organs are dilated at their distal ends, between the seeds, so as to form a continuous envelope, only interrupted by narrow pits, into which the seeds exactly fit (see Figs. 202 and 203, A). In the lower part of the fruit, below the region of the seeds, the pericarp is formed by the union of the outer and shorter scales. In order to make the somewhat complicated arrangement more intelligible, we may further quote Count Solms-Laubach's summary:—"We have in the fructification (spadix) two kinds of organs of different character and closely crowded together: the seed-stalks (cords) [our pedicels] diverging above, clusterwise, and each terminating in a seed; and the interstitial organs [our interseminal scales], increasing constantly in length from the periphery of the cluster towards the inside, appearing by themselves in the periphery, but mixed with the seed-stalks further in, overtopping the seeds with their apices, and forming by the union of their apices the homogeneous tissue-layer of the surface of the fructification. In consequence of this arrangement, every seed is sunk in a pit, the orifice of which then narrows over the seed, owing to the lateral outgrowth of its walls."[1]

This description should be compared with the diagram, Fig. 203, A, and with the more detailed Figs. 202, 203, D, and 204. We will now take the

[1] *Annals of Botany*, vol. v. 1891, p. 446.

various constituent organs of the fruit, and consider their structure a little more in detail.

The receptacle forms, as we have seen, the enlarged termination of the axis of the fruit. The peduncle has a structure like that of the stem, on a small scale, and the bundles given off to the bracts divide up like those of the vegetative leaves, though only to a small extent. A remarkable feature in the anatomy of the peduncle is the great development of the phloëm, which much exceeds the wood in thickness. This peculiarity, which recurs in some of the American species, may be explained by the great demands on the organic food-supply made by the crowded reproductive organs, and especially by the seeds. The receptacle itself is poorly preserved, but shows here and there sections of collateral vascular bundles, on their way out to the appendages.

The bracts have, on the whole, the structure of reduced foliage-leaves. Their outer surface is clothed by ramenta, and stomata have been detected in their epidermis.[1] Towards the inner surface of the bract, the mesophyll has a fibrous structure, but the bulk of the parenchyma is formed of short cells with a curious scalariform thickening on their walls. Several large gum-canals traverse the bract, which in this species usually contains three vascular bundles. These bundles are reduced in structure, but near the base, where they are best developed, they seem to be of the mesarch type usual in the foliar bundles of Cycads.

The seed-pedicels, which are seen in great numbers in the transverse section of the fruit (see Fig. 204),

[1] C. A. Barber, in MS.

have an approximately cylindrical form, with their sides somewhat flattened by pressure. Through the middle of each pedicel runs a vascular bundle, which, so far as the preservation allows of an opinion, appears to have had a concentric structure. Outside the vascular strand is a well-marked bundle-sheath, suc-

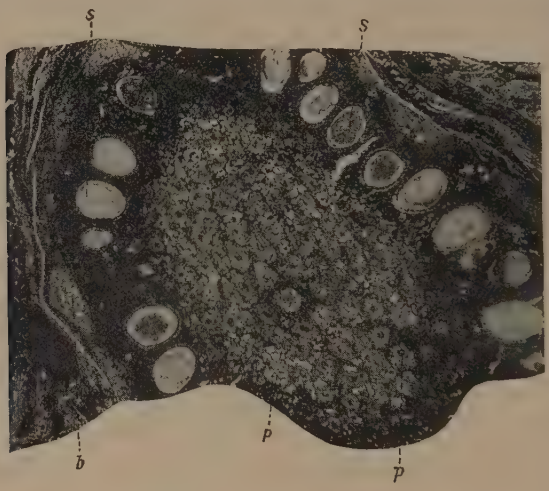

FIG. 204.—*Bennettites Gibsonianus*.—Transverse section of fruit, not quite complete. *b*, bracts; *s*, seeds, ranged in a ring around the fructification; *p*, pedicels, belonging to other seeds, borne at a higher level; between the pedicels the interseminal scales can be recognised. The pericarp is the dark zone in which the seeds are embedded. × about 3. From a photograph by Dr. Bousfield. S. Coll. 350.

ceeded by a wide cortex.[1] The surrounding epidermis belongs in reality, as Dr. Wieland has shown, to the adjacent interseminal scales.

Each pedicel terminates directly in an orthotropous seed. The xylem of the bundle ends at the chalaza

[1] It is possible, however, that the "bundle-sheath" is really the epidermis, and that the so-called "cortex" is built up of epidermal appendages.

in a small disc, while the adjacent tissues of the pedicel pass over into the testa. The seeds have a length of over 3 mm., not counting the micropylar tube, and a diameter of nearly 2 mm. The seeds which have been investigated were fully ripe, for each, when well preserved, contains a large embryo, nearly filling the cavity (see Figs. 204, *s*, 203, C, and 205). The testa is made up of three layers, an inner and outer layer of small comparatively thin-walled cells, and a middle layer of large square or palisade-like cells, which appear almost solid, an appearance which may be due to extreme thickening of their cell-walls (Fig. 203, C and D).

Towards the micropyle, the middle layer of the testa is greatly dilated, and is here several cells in thickness ; it is surrounded by the external zone, which in this part is very distinct (Fig. 203, D). The inner layer of the testa forms the internal tube of the actual micropyle, which, however, in these ripe seeds is closed, as is usually the case (see Fig. 203, D, which represents a somewhat oblique longitudinal section through the micropylar end of a seed). The distal end of the micropyle (not shown in our figure) narrows out considerably, owing to reduction of the middle layer of cells, but appears to be somewhat dilated again at the extremity. The testa is everywhere closely adherent to the surrounding tissue of the pericarp. In the body of the seed, the nucellus is only to be traced as a structureless membrane (see Fig. 203, C, *n*), but it is better preserved at the apex (Fig. 203, D, *m*).

The embryo so nearly fills the cavity of the seed that the latter may be spoken of as exalbuminous,

though it is quite possible that here, as in most so-called exalbuminous seeds, some slight remains of the endosperm persisted. The small mass of tissue marked *e* in Fig. 203, D, in which the nuclei appear to be preserved, may probably be a portion of the remaining endosperm, though it might also be interpreted as belonging to the root-cap of the embryonic radicle.

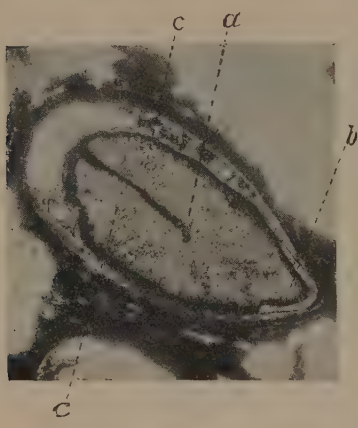

FIG. 205.—*Bennettites Gibsonianus.* Longitudinal section of seed, showing dicotyledonous embryo. *c*, *c*, the two cotyledons; *a*, apex of plumule; *b*, radicle. × 12. From a photograph by Dr. Bousfield. S. Coll. 351.

The embryo is very well preserved, indeed the Bennettiteae afford the only cases in which it has been possible to study the embryos of fossil plants in detail. The embryo is a typical dicotyledonous one, with the pointed radicle directed towards the micropyle. The hypocotyl is short; more than half the whole length of the embryo is occupied by the two thick cotyledons, the surfaces of which are in contact (see Figs. 203, C, 205). Between them, the growing point of the plumule has been recognised in favourable preparations (Fig. 205, *a*). The tissue of the embryo is to some extent preserved, and the position of the young vascular bundles in the cotyledons can be determined (see Fig. 203, C, which represents a seed in transverse section, passing through the two cotyledons, *ct*). The vascular cylinder of the hypocotyl has also been

recognised, and its connection with the cotyledonary bundles traced.[1] The number of seeds in which the embryo is well preserved is so considerable as to leave no doubt regarding the correct interpretation of the main facts. The general structure of the dicotyledonous embryo is in no way surprising in a plant of Cycadean affinities, but the practically exalbuminous character of the seed is without example among recent Gymnosperms. Of course, in speaking of Bennettiteae as Gymnosperms, we are referring rather to their presumed affinities than to the actual structure of the fruit, which comes very near to being angiospermous.

The interseminal scales, which combine to form the pericarp, have proved difficult to investigate, owing to their state of preservation. In their lower part, where they pass between the pedicels of the seeds, they are crushed out of shape, and much disorganised, so as to be reduced in many cases to a vascular bundle with an irregular epidermis loosely surrounding it, the intermediate tissue having disappeared. The interseminal scales are somewhat similar in structure to the pedicels of the seeds, but the homologies of their respective tissues are not yet clearly understood.

The expanded outer ends of the interseminal scales unite to form the "pericarp," a dense, apparently continuous zone, starting at the base of the fruit, from the sides of the receptacle, and extending, with increased thickness, over the top. In its upper portion, as already explained, it encloses the seeds, and is perforated by their micropyles. Its external surface is furrowed, the furrows forming a network.

[1] Solms-Laubach, *l.c.* p. 440.

The pericarp, from its dense structure, has at first sight the appearance of a distinct organ of the fruit, but, as above stated, there is no doubt that it is in reality built up of the distal parts of the interseminal scales (Fig. 203, A). The furrows thus correspond to the lines of junction of the constituent scales. The outer surface is coated by a distinct epidermis, which extends into, and lines the furrows (see Fig. 203, D, *c*). The inner tissue of the pericarp-zone (*p*) is formed of parenchymatous cells, with moderately thick walls, and abundant dark contents, perhaps indicating the presence of some reserve food-substance during life. Tangential sections of the upper part of the fruit show the micropyles of the seeds, lying at the angles where the limits of the constituent interseminal organs meet. In Fig. 203, D (from a radial section), two of the furrows marking these limits (*c*) are shown close together, having been cut at a short distance from the micropyle towards which they converged. Vascular bundles run out into the pericarp between the seeds, and are the continuation of those seen in the lower portion of the interseminal scales.

So far as the bracts and gynæcium are concerned, the classic *Bennettites Gibsonianus* may still serve as a type of the complex Bennettitean fructification. Other similar European examples have been described, among which one from the Oxford Oolite of Normandy, called *Bennettites Morierei*, was fully investigated by Professor Lignier of Caen.[1] The specimen is a detached fruit, not known in connection with the stem

[1] O. Lignier, *Végétaux fossiles de Normandie*, "Structure et affinités du *Bennettites Morierei*," Caen, 1894.

on which it grew. It has hence been supposed that it may have had a longer stalk than that of *B. Gibsonianus*, and so may have been more easily detached. A Cycadean stem (*Fittonia Brongniartii* of Saporta), to which it may possibly have belonged, was found in the same locality. The fruit is somewhat larger than in our English species, with which, however, it agrees in all essential points of structure. The exceptionally beautiful preservation enabled Professor Lignier to work out the details of structure with remarkable precision.

It is, however, to the investigation of the magnificent American material that the recent remarkable progress in our knowledge of Mesozoic Cycadophyta is principally due, and some account of the chief results attained must now be attempted.

As regards habit, the American, like the contemporary European Cycadophyta, seem to have been plants of no great stature; there is no evidence at present for trunks of a height of more than 10 or 12 feet, while the great majority of the stems were quite short, like that shown in Fig. 199. In some cases the stems were nearly spherical; often several are connected together as branches of the same stock. In seeking analogies among recent Cycads we must therefore go to the shorter-stemmed genera, such as *Bowenia* or *Stangeria*, or perhaps *Macrozamia*, rather than to tall plants like *Microcycas* and various species of *Cycas*.

So far as the foliage and the external features of the trunk are concerned, the remarks made at the beginning of the chapter apply to the American as well as to the European forms. The majority of the latter

are included by their investigators in Buckland's genus *Cycadeoidea* (synonymous with *Bennettites* of Carruthers [1]), but a new genus, *Cycadella*, has been founded by Lester Ward for a number of dwarf stems, distinguished by their abundant ramental covering, which often envelopes the trunk ; twenty species have been referred to this genus, which is characteristic of somewhat older beds than those in which *Cycadeoidea* is prevalent.

Anatomically, the American stems so far investigated agree wonderfully closely, often down to the most minute detail, with the European species of *Bennettites*. It is, however, quite probable that when the investigation of the vast material has proceeded further, more variety may be found. As regards the form and structure of the leaves of the Bennettiteae, practically all our information comes from Dr. Wieland, who in various specimens has succeeded in finding the young leaves still folded in the bud and preserved in great perfection. His observations were chiefly made on *Cycadeoidea ingens*, a species in which he estimates the length of the mature leaf at about 10 feet, and on *Cycadella ramentosa*, a much smaller plant, so that both the later and the earlier types are represented. It is sufficient, without going into details, to say that Dr. Wieland's investigations show that in form, prefoliation, venation, and anatomical structure these leaves show a

[1] The name *Cycadeoidea* is employed by some European writers for trunks of the Bennettitean type without fructifications, as in the case of Professor Seward's *Cycadeoidea ingens*. In discussing the American species, I follow the usage of the palæobotanists of that continent, employing the names *Cycadeoidea* and *Cycadella* throughout. It is desirable, however, that an agreement as to the nomenclature should be arrived at.

close agreement with those of recent Cycads of the suborder Zamieae; the vascular bundles were collateral and mesarch, without radial arrangement of the centrifugal wood or phloëm. Speaking especially of *Cycadeoidea ingens*, Dr. Wieland says, "Were one to adjudge the taxonomic position of the fossil species on the basis of its foliage only, one might, bearing in mind the general absence of scale-leaves, place it near *Macrozamia* or *Encephalartos*."[1] The leaves of *Cycadella* only differ in details; the structure of the pinnules is found to be almost identical with that in the recent *Bowenia*.[2] This close correspondence in foliar characters with the recent Cycadaceae is the more remarkable when we consider how totally the two groups differed in their reproductive organs, the organisation of which has only been fully revealed by Dr. Wieland's researches.

The European specimens had yielded scarcely any information as to the nature of the microsporangiate organs of the Bennettiteae. In an Italian species, *Cycadeoidea etrusca*,[3] bodies interpreted as pollen-grains were discovered by Count Solms-Laubach in the interior of a fructification, lying in the space between the apex of the ovuliferous receptacle and the surrounding bracts. Though, owing to bad preservation, the stamens were not detected, the inference was drawn that they

[1] *American Fossil Cycads*, p. 94. [2] *L.c.* p. 101.

[3] The specimen was found on an Etruscan tomb at Marzabotto near Bologna; Capellini and Solms-Laubach, "I tronchi di Bennettitee dei Musei Italiani," *Mem. d. R. Accad. delle Sc. dell' Ist. di Bologna*, series v. vol. ii. 1892. Dr. Wieland, who has since reinvestigated the fructifications and found some further remains of structure, compares them with those of *Cycadella*. See his "Historic Fossil Cycads," *Amer. Journal of Science*, vol. xxv. February 1908, p. 93.

were probably borne in the same fructification with the ovules. This suggestion has been completely confirmed by the investigation of the perfectly preserved specimens which have since come to light in America.

The male sporophylls of the Bennettiteae were first discovered in 1899, in the Dakota species *Cycadeoidea ingens*, already referred to;[1] their relation to the gynæcium was established two years later, in the same species, when the organisation of the hermaphrodite or bisexual flower was described for the first time.[2] Twenty-five trunks with bisexual fructifications, belonging to seven American species, have now been investigated. The fructifications were borne laterally on the stem, precisely in the same way as those of *Bennettites Gibsonianus* and other European forms, which were probably also bisexual (see p. 588). The plant bore a considerable number of fructifications at the same time (see Fig. 199); on a single specimen of *Cycadeoidea dacotensis* sixty-one fruits, all more or less at the same stage of development, were counted, and Dr. Wieland is inclined to think that the plants were "monocarpic," fruiting once for all and then perishing, as is the case with many Palms and Bamboos at the present day.

The structure of the bisexual fructification or "flower," as it may be appropriately called, will first be described in the case of *Cycadeoidea dacotensis*, one of the species most fully investigated. It may, however, be said at once that no important differences in

[1] Wieland, "A Study of some American Fossil Cycads, Part i. The Male Flower of *Cycadeoidea*," *Amer. Journ. Science*, vii. 1899.

[2] *L.c.* Part iv. "On the Microsporangiate Fructification of *Cycadeoidea*," *Amer. Journ. Science*, xi. 1901.

the floral morphology of the different species have been detected.

The whole fructification has a length of about

FIG. 206.—*Cycadeoidea dacotensis.*—Median longitudinal section of a bisexual flower. The peduncle, with the surrounding leaf-bases and bracts, is drawn from one section; the ovulate cone and microsporophylls are drawn from several other sections of similar strobili. *s*, the incurved microsporophylls; *o*, the ovuliferous cone; *a*, eroded outer border of the armour and bracts, forming the trunk-surface; *r*, ramentum between outermost bracts and adjacent leaf-base; *l*, leaf-base; *c*, cortex of trunk; *t*, bundles supplying peduncle. About ⅔ natural size. From Wieland.

12 cm., protruding somewhat beyond the leaf-bases of the trunk. (See the restored section shown in Fig. 206.) About half this length consists of the stout peduncle, which bears 100 or more spirally arranged

bracts on its upper part. The centre of the flower is occupied by the ovuliferous receptacle, about 4 cm. in height, terminating the peduncle, as in *Bennettites Gibsonianus* (cf. Fig. 203, A). In *C. dacotensis*, however, the form of the receptacle is much more acutely conical, and the stage of development, in the present case, is a far earlier one, minute immature ovules taking the place of the ripe seeds of the specimens previously described.

The stalked ovules and interseminal scales here form a layer only 1.5 mm. in height (see Fig. 207, where this zone is better shown), whereas in the mature seed-bearing condition these organs have grown to at least ten times the length. We have, in fact, at the stage now under consideration, to do with a *flower*, while the fructification of *Bennettites Gibsonianus*, described above, was already a *fruit*. The receptacle bears ovules in its middle region; the base and apex are sterile, and clothed only with the barren interseminal scales, which at the apex are prolonged into a tuft (Fig. 207). The details of structure of the ovules at this stage have not yet been published.

Surrounding the ovuliferous cone, and enclosed by the bracts, is the whorl of compound microsporophylls which forms the most striking feature of the flower. The microsporophylls, or stamens, are numerous, numbering from eighteen to twenty in *C. dacotensis*, and are ranged in a single verticil; they are inserted hypogynously, below the base of the gynæcium (see Fig. 206), and their stalks are united to form a continuous sheath (the "disc" of Wieland), like the monadelphous stamens of a Mallow. (see diagrams,

Figs. 208 and 209). The connate sheath extends up to about the height of the top of the gynæcium; at this level the stamens become free from each other; they are large and complex structures about 10 cm. in length, if straightened out; they are always found,

FIG. 207.—*Cycadeoidea dacotensis*.—Longitudinal section through the summit of an unexpanded bisexual flower. In the middle is the upper part of the ovuliferous cone, showing the zone of ovules and interseminal scales and the terminal tuft. To the right and left the compound stamens are seen, with their tips infolded parallel to the sides of the central cone. The upper curved portion of each stamen is missing (cf. Fig. 206, *s*). The pinnæ, each bearing a series of synangia, are cut longitudinally. On the outside of all are the bracts. × 2. From a photograph. After Wieland.

however, to be infolded in a circinate manner, the sporophylls curving over towards the gynæcium, so that their deflexed tips reach down almost to its base (see Figs. 206 and 207). Each stamen is a pinnately compound leaf with about twenty pairs of alternate

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pinnæ, directed inwards from the concave side of the whole organ (Figs. 206 and 207; cf. the diagrams, Figs. 208 and 209). The apical and basal pinnæ are sterile; all the rest bear synangia, arranged in two rows, the synangia numbering about ten in each row

FIG. 208.—*Cycadeoidea ingens*.—Restoration of an expanded bisexual flower in longitudinal section, showing the central ovuliferous cone, the hypogynous whorl of pinnately compound stamens, bearing numerous synangia, and the surrounding bracts, hairy with ramenta. About half natural size. From Wieland.

in the case of the longest pinnæ. If, with Dr. Wieland, we regard each synangium as representing a reduced pinnule, the whole sporophyll must be called bipinnate. The stamen was thus a highly complex organ, recalling the fertile frond of a Fern rather than the comparatively simple type of microsporophyll which we meet with in the stamens of the higher plants. The elaborate

organisation of the whole flower is well shown in the diagrammatic figures 208 and 209, drawn by Dr. Wieland to represent the flower in an expanded condition.

FIG. 209.—*Cycadeoidea ingens.*—Plan of the bisexual flower, showing the central ovuliferous cone, the whorl of thirteen compound stamens, united at the base, and bearing synangia on their pinnæ, and a series of the hairy bracts. The diagram is about on the same scale as Fig. 208, and shows the flower as it would appear, seen from above, if all its parts were fully expanded. From Wieland.

These diagrams are based on the species *Cycadeoidea ingens*, in which the number of stamens is less than in *C. dacotensis*. It will be noticed that the arrangement of the parts is just the same as in a typical Angiospermous

flower, with a central superior gynæcium, a whorl of hypogynous stamens, and an enveloping perianth.

The anatomical structure of the microsporophylls has not yet been fully investigated, but it is known that two ranks of vascular bundles are present in the connate disc, and that a considerable number

FIG. 210.—*Cycadeoidea dacotensis.*—Transverse section through rachis of a sporophyll and adjacent synangia. The middle and lower synangia are cut transversely, the upper very obliquely. The palisade-layer, walls of the loculi, and spores are all shown. × about 25. From Wieland.

enter each rachis as it becomes free. The general arrangement of the bundles is compared with that in the rachis of a Cycad leaf.

The synangia, as already mentioned, are inserted in two rows on each pinna ; their insertion is described by Dr. Wieland as "sub-lateral." Such a position is common on the modified fertile fronds of Ferns, where the insertion of the sporangia on the lower surface, usual

in the case of unreduced sporophylls, is often departed from. The shortly-stalked synangia are much broader than long, contain two rows of loculi (Figs. 210 and 211), and closely resemble those of certain Marattiaceae, simulating in a remarkable degree the stalked synangia of *Marattia Kaulfussii*.[1] The analogy of this species, though not of any special taxonomic significance, shows that there is no absolute necessity to regard the pedicellate synangia of the Bennettiteae as representing distinct leaflets.

The form of the synangia in *Cycadeoidea* is somewhat affected by their crowded arrangement in the limited space afforded by the infolded sporophyll (Fig. 210).

The synangia shown in Fig. 210 are for the most part cut transversely, showing the full number (20-30) of the loculi, while Fig. 211 represents a single synangium cut longitudinally through the short stalk, in a plane at right angles to the rows of loculi, so that two loculi only are shown. The exterior of the synangium is formed by a well-developed

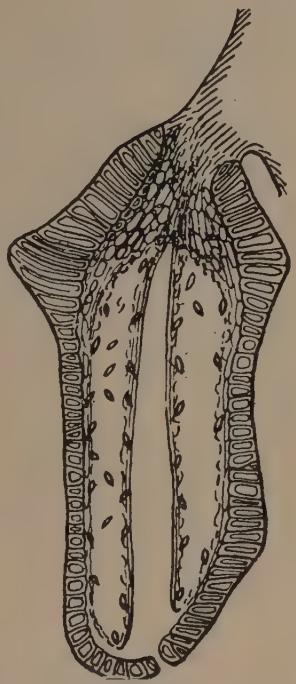

FIG. 211.—Longitudinal section of a synangium, showing short stalk attaching it to rachis. The "buttressing" of the basal part of the wall is shown; also two loculi, in longitudinal section, containing some pollen-grains. Dehiscence appears to have begun. × 40. From Wieland.

[1] See Christ, *Farnkräuter der Erde*, p. 359, Fig. 1129, 1897.

palisade-layer, thickened near the base (Fig. 211); this is lined by a layer of small, thin-walled cells, which also form the inner walls of the loculi (Fig. 210). In dehiscence the two rows of loculi appear to have split apart, the synangium thus opening by two valves, while the individual loculi dehisced by longitudinal slits (Figs. 210 and 211). If this was the case, the resemblance to *Marattia* extended to the mode of dehiscence.

The microspores or pollen-grains have been carefully examined by Dr. Wieland, but without finding any decisive proof of the presence of antheridial cells. In size the microspores are intermediate between those of Cordaiteae and recent Cycads.

As already mentioned, the variation in structure among the flowers of the American Bennettiteae, so far investigated, is unimportant; neither do their flowers differ essentially, as it appears, from those of such European species as *Bennettites Gibsonianus* and *B. Morierei*. The group, in fact, was morphologically a narrow one, however rich in specific forms. The smallest number of stamens observed was ten, in *Cycadeoidea Jenneyana*. The discovery of the bisexual flower of *Cycadeiodea Paynei* is of interest, because in the form of the receptacle and other characters this species agrees so closely with *Bennettites Gibsonianus* as to leave no reasonable doubt that the flowers of the British species were likewise bisexual, the absence of stamens in the specimens observed being simply due to the maturity of the fruit at the time of fossilisation. The same applies to *Bennettites Morierei*, and indeed it is quite probable, though not yet demonstrated, that all Bennettiteae had bisexual flowers. In many

strobili, both young and old, where the stamens were not preserved, Dr. Wieland was able to detect the remains of the staminate disc, seated on the rim of the receptacle. The genus *Cycadella* appears to have had precisely the same floral structure as *Cycadeoidea*. In a very small fructification of *Cycadella wyomingensis*, only 7 mm. in diameter, a whorl of thirteen stamens, surrounding the central receptacle, was found, just as in *Cycadeoidea ingens*.

From the comparison of the younger and older stages (as, for example, in *C. dacotensis*), it appears that as the fruit matured the expanding gynæcium encroached on and ultimately filled the space originally occupied by the whorl of stamens. Dr. Wieland inclines to the view that the flowers were protandrous, the pollen being ripe before the ovules were ready for fertilisation; a detailed knowledge of the condition of the ovules in flowers of different ages will be necessary before this point can be decided. In a magnificent fossil Cycad, *Cycadeoidea Reichenbachiana*, found about the year 1753 near Cracow in Poland, and probably of Lower Cretaceous age, Dr. Wieland has recently demonstrated the bisexual structure of the flowers, which appear to agree in all essential points with those of *C. dacotensis*; the number of stamens in a whorl is sixteen in *C. Reichenbachiana*. This is the first time that the presence of bisexual flowers, like those of the American Cycadophytes, has been clearly observed in a European species, though, as we have seen, the indirect evidence left little doubt as to the facts.[1]

[1] Wieland, *Historic Fossil Cycads*, above cited. See also F. Lester Ward, "A Famous Fossil Cycad," *Amer. Journ. of Science*, vol. xviii. 1904.

Many years before the existence of such a family as that of the Bennettiteae was even suspected, certain remarkable fossils were described from the Lower Oolite of the Yorkshire coast, under the name of *Zamia gigas*.[1] The fullest account of these fossils is that presented by Williamson to the Linnean Society in 1868. Our Fig. 212 (from Williamson's memoir) represents the plant in a restoration which has been proved by more recent investigations to be essentially correct. Mr. Carruthers, in his paper on Cycadean stems above referred to, established the new genus *Williamsonia* for the reception of *Zamia gigas* and allied forms, and this name is the one now used.[2]

The various organs of the plant are, as usual among fossils, almost always found separately. They consist of the large *Zamia*-like leaves (from which the old generic name was taken), portions of the stem, covered with the rhomboidal leaf-scars, and lastly the fructifications, with the long scaly stalks on which they were borne. Williamson pieced these various parts together, as shown in his restoration, and Brongniart confirmed his conclusions, but other authorities entirely rejected them, regarding the fructifications as those of Monocotyledons, and as having nothing to do with the Cycadean foliage or stem. Williamson's view has proved to be the correct one.

The fructification of *Williamsonia* is in size and appearance something like a common artichoke, and

[1] Lindley and Hutton, *Fossil Flora of Great Britain*, 1830. Originally figured by Young and Bird, *Geological Survey of the Yorkshire Coast*, 1822.

[2] Williamson, "Contributions towards the History of *Zamia gigas*," *Linnean Society's Transactions*, vol. xxvi. (published 1870); Carruthers, *l.c.*, in same volume.

was borne at the end of a long stalk, 20 or 30 cm. in length, covered with spirally arranged scale-leaves.

FIG. 212.—*Williamsonia gigas*.—Williamson's original restoration of the plant, showing the upright stem, with rhomboidal leaf-scars, the crown of *Zamia*-like leaves, and the scaly, spherical fructifications. From the *Linnean Soc. Trans.*

The exterior of the globular fructification was formed by the overlapping, involucral bracts. No petrified

specimens appear to be known, but the structure has now been interpreted with considerable probability, in the light of that of the hermaphrodite flowers of *Cycadeoidea*. The middle of the fruit is occupied by a stout pyriform axis, which no doubt represents the central ovuliferous receptacle, while traces of the surrounding stamens have also been detected. Williamson described some forms of fructification as male and others as female, but they, in all probability, represent merely different states of preservation of the same bisexual flowers. Details will be found in Wieland's *American Fossil Cycads*.[1]

Professor Seward, from the study of an English specimen now at Paris, as well as from other evidence, proved conclusively that the *Williamsonia* fructifications and the *Zamia*-like leaves were borne on the same stem.[2] He regarded the plant as closely allied to *Bennettites*,[3] and this view has proved to be fully justified, though the degree of relationship can only be determined when specimens of *Williamsonia* are discovered with microscopic structure preserved. On present evidence, it appears most probable that *Williamsonia* (of which several species, from various parts of the world, extending to North America and India, are known) belonged to the Bennettitales, differing from *Bennettites* chiefly in the long peduncles on which the fructifications were borne, and in the taller and more slender stem.

[1] See especially his Plate xlvi. with the description of figures.

[2] Seward, "On the Leaves of *Bennettites*," *Proc. Cambridge Phil. Soc.* vol. ix. p. 273, 1897. The critical specimen, showing both leaves and floral peduncles in connection with the stem, has been refigured by Wieland in his paper on *Historic Fossil Cycads*, above cited.

[3] See his *Catalogue of Mesozoic Plants: Fossil Plants of the Wealden*, Part ii. 1895, and *Jurassic Flora*, Part i. 1900.

A very interesting Cycadophyte, from the Rhætic of Southern Sweden, has been described by Professor Nathorst, under the name *Williamsonia angustifolia*.[1] The stems are long and slender and repeatedly forked by "false dichotomy," a flower usually terminating the axis between the two branches. The floral structure, so far as the material allows of its investigation, appears to be that of a *Williamsonia*, though the flowers are on a small scale compared with those of *W. gigas*. The flowers were described by the discoverer as male and female, but now that the bisexual flowers of Bennettiteae are known, it appears most probable that in this species also they were all of one kind, the differences observed being due merely to the stage of development and state of preservation. This is rendered the more likely by the fact that the flowers originally described as male, in some cases distinctly show the central (presumably ovuliferous) receptacle. The leaves, which occurred chiefly in rosettes at the points of branching of the stem, were narrow and pinnate, of the form known as *Anomozamites*,[2] and were of small size, about 7 or 8 cm. in length. The habit of the plant is totally unlike that of Cycadaceae or of the typical Bennettiteae, and has suggested the possibility of a nearer approach to the Angiosperms than is shown by other Mesozoic Cycadophyta.

[1] A. G. Nathorst, "Beiträge z. Kenntnis einiger mesozoischen Cycadophyten," *Kongl. Svenska Vetenskaps Akad. Handl.* vol. xxxvi. No. 4, 1902, and the earlier papers there cited.

[2] The plant is referred to *Anomozamites minor* (Brongn.), the name used by Dr. Wieland.

2. *Cycadaceae.*—Side by side with the Bennettiteae, true Cycadaceae, or closely allied plants, probably existed in Mesozoic times, but the evidence for their presence is scanty in the extreme.

Male cones, of a Cycadean type, have been recorded under the name of *Androstrobus*, as, for example, *A. Nathorsti*, a species from the Wealden of Sussex, described by Professor Seward.[1] The thick axis of this cone bears spirally arranged, more or less triangular scales or sporophylls, 1 to 1.5 cm. in length. "Towards one end of the specimen the basal part of a scale is seen in surface view, and on it are clearly preserved what are taken to be the outlines of pollen-sacs. . . . The striking regularity with which these impressions are arranged is much more marked than in the pollen-sacs of recent Cycads. On the lower surface of a staminal leaf of *Dioon* or *Encephalartos*, we find, on the removal of the pollen-sacs, a fairly distinct reticulate marking, but of much less regularity than in the fossil."[2] From the evidence of this specimen and one or two similar fossils, it has been inferred that male cones, not essentially different from those of living Cycads, occurred in Mesozoic floras. The evidence, however, is not wholly convincing, and has been considerably shaken by Professor Nathorst's discovery that a cone originally described by him as *Androstrobus Scotti*, and referred to Cycadaceae, was in reality a Lycopodineous fructification with megaspores, for which he has now created the new genus *Lycostrobus*.[3]

[1] *Fossil Plants of the Wealden*, Part ii. p. 110.

[2] Seward, *l.c.* p. 111.

[3] A. G. Nathorst, "Paläobotanische Mitteilungen, 3. *Lycostrobus Scotti*," *Kongl. Svenska Vetenskaps Akad. Handl.* vol. xliii. No. 3, 1908.

As regards female cones of the Cycadaceae, such as are characteristic of the recent suborder Zamieae, the fossil evidence is unsatisfactory. It is quite probable that cones of this kind may occur in various Mesozoic deposits, but, generally speaking, the state of preservation of such specimens is so poor that it is impossible to distinguish them with any certainty from Coniferous strobili of similar habit.[1]

We have already seen (Chapter XI. p. 493) that fructifications, possibly referable to Cycadophyta, occur even in the Permian beds, though their true affinity is an open question.

The recent genus *Cycas* differs entirely from other members of the Order in the structure of the female fructification. The carpels are among the most characteristic of vegetable organs, and fossils resembling them have been recorded from various Mesozoic strata. In at least one case (*Cycadospadix Hennoquei*, Saporta, from the Lower Lias) the carpel, fimbriated like that of *Cycas revoluta*, has a seed still attached.[2] The evidence for the existence of near allies of *Cycas* in Mesozoic times so far seems strong, but, on the other hand, much doubt has recently been cast on the

[1] Cf. Seward, *Fossil Plants of Wealden*, Part ii. p. 113. One of the most perfect specimens attributed to the Zamieae is the *Beania gracilis* of Carruthers ("On *Beania*, a New Genus of Cycadean Fruits from the Yorkshire Oolites," *Geol. Mag.* vol. vi. 1869), which consists of an elongated axis, bearing a number of peltate sporophylls, on each of which two seeds are inserted. The sporophylls themselves agree closely with those of a recent *Zamia*, but they are much more remote from each other than in that genus. Professor Seward is inclined to regard *Beania* as more probably belonging to Ginkgoaceae than to the Cycads. See Seward and Gowan, "The Maidenhair Tree," *Annals of Botany*, vol. xiv. 1900. Also Seward, *Jurassic Flora*, Part i. 1900, p. 272.

[2] See Saporta et Marion, *L'évolution du règne vegetal, Les Phanérogames*, t. i. p. 111, Fig. 59, A, 1885.

nature of the leaves referred to *Cycas* or *Cycadites*, with which the carpels are sometimes associated. Professor Nathorst[1] has shown that in several species from the Cretaceous of Greenland, formerly placed in the genus *Cycas*, the vascular bundle of the pinna was not single, as in the recent genus, but double, and that the distribution of the stomata was also quite unlike that in *Cycas*. He has therefore placed these forms in a new genus, *Pseudocycas*, and no longer regards them as belonging to the same suborder as *Cycas*. It is probable that the species now placed in *Cycadites* may prove to have similar peculiarities.

Thus the whole question of the existence of Mesozoic Cycadaceae, whether of the suborder Zamieae or Cycadeae, is in an unsatisfactory position and the positive evidence singularly meagre. There are a great number of Cycad-like fossil remains, known only as impressions and casts, the true nature of which must remain doubtful until specimens showing structure come to light. At present such specimens, of Mesozoic age, are almost wholly limited to the Bennettiteae.

3. *Affinities of Mesozoic Cycadophyta.*—The Cycadophyta of Nathorst form a main subdivision of the Gymnosperms, including the Cycadales, the Bennettitales, and no doubt other groups, which we are not yet in a position to characterise.[2] The Cycadales correspond simply to the Order Cycadaceae, with the two well-known suborders Cycadeae and Zamieae;

[1] A. G. Nathorst, "Paläobotanische Mitteilungen, 1. *Pseudocycas*," *Kongl. Svenska Vetenskaps Akad. Handl.* vol. xlii. No. 5, 1907. The cuticle of carbonised specimens was examined microscopically.

[2] Nathorst, "Beitr. z. Kenntnis d. mesozoischen Cycadophyten," p. 3.

in like manner the limits of the Bennettitales are at present identical with those of the Bennettiteae, if we include the Williamsonieae, which should perhaps count as a distinct Order or Sub-order.

Throughout our description of the Bennettiteae we have assumed that these plants really had affinity with Cycads. The sum of their vegetative characters can leave no doubt that this supposition is justified, but it is a striking fact that in their reproductive organs, that is to say, in the very characters on which systematists are accustomed to rely, the Bennettiteae differ *toto coelo* from the Cycadaceae. The organisation of the flower is so different from that of the cones of any recent Cycad that it is difficult to determine with any certainty the homologies of the parts in the two groups. It is, of course, possible that future palæontological discoveries may reveal the existence of types of fructification intermediate between those of Cycadales and Bennettitales; at present, however, it seems as if their development had followed different lines from a very early stage.

The points in which Bennettitales agree with Cycadales are, the form and general structure of the stem, the histological details of its tissues, the arrangement of the leaves, their form and minute structure; in all these respects the agreement is exact, so far as the existing investigations on American and European species enable us to judge. The only differences worth mentioning, in the vegetative organs, are the simpler course of the leaf-trace bundles in Bennettitales, and the presence of ramenta like those of Ferns, instead of the woolly hairs of Cycads. In these two

respects the Bennettitales appear to be more primitive than the sister class. It has been suggested by Dr. Wieland that in Triassic times there may not yet have been any definite border-line between the two classes, so far as vegetative features are concerned.[1] In *Anomozamites minor* (*Williamsonia angustifolia* of Nathorst), the oldest known member of the Bennettitales, the habit was equally unlike that of typical Cycadaceae and of typical Bennettiteae. It has recently been suggested that an abortive bud occurring beneath the peduncle of the cone in the recent Cycad *Dioon* is the second lateral branch of the primitive dichasium, an interpretation which would tend to bring the Cycadaceous morphology a step nearer to the type of *Anomozamites*.[2]

On the other hand, the fructifications are on a far higher level of complexity in the Bennettitales. The lateral, probably axillary position of the fertile shoots (flowers) is the first difference to be noted. As Dr. Wieland puts it (p. 229), the Bennettitales have seized on the lateral bud as a means of fructification, thus ensuring the production of more numerous strobili. That the axis of the inflorescence is a modified branch of the stem is clear; the enveloping bracts are, no doubt, modified leaves or possibly leaf-bases, and likewise present no difficulty. We might well compare them to the scale-leaves, in which the young cone of an ordinary Cycad is enwrapped. It is when we come

[1] *American Fossil Cycads*, p. 228. The author gives a very full comparison between the two groups, as regards both vegetative and reproductive characters, in his Chapter IX.

[2] F. W. South and R. H. Compton, "Anatomy of *Dioon edule*," *New Phytologist*, vol. vii. Dec. 1908, p. 225.

to the internal organs of the fructification—the stamens, the seed-pedicels, and the interseminal scales—that difficulties begin.

There appears to be no doubt as to the morphological nature of the stamens, which are clearly sporophylls of a highly complex and leaf-like character, borne directly on the axis of the fructification. So far, then, as the androecium is concerned, the Bennettitean strobilus is admittedly a *flower*. The organs of the gynæcium, however, have received various interpretations, which may be grouped under two heads. Either all the organs (seed-pedicels and interseminal scales) are of a foliar nature, in which case the fructification throughout is comparable to a flower, or the seed-pedicels are axial structures,[1] and this part of the fructification is an "inflorescence." The question is important on account of the comparison with the Angiosperms, on which much stress has been laid by recent writers. We will first consider the second view, of which Professor Lignier is the chief advocate. On his interpretation the interseminal scales are modified leaves, homologous with the bracts, and ultimately with the foliage leaves, while each seed-pedicel is a sporophyll borne on a unifoliar bud, which is probably axillary to an interseminal scale. Professor Lignier points out the analogy which, on his view, exists between the strobilus (or rather the female part of it) and the vegetative stem, in which also only a minority of the leaves have buds (usually fructifications) in their axis. The unifoliar bud, which would thus represent a female flower,

[1] The third view mentioned as possible by Count Solms-Laubach, that the interseminal scales are also axial, does not seem to be upheld.

is, of course, extremely reduced.[1] The analogy with the main stem is the strongest point in this interpretation, but it appears to be open to three serious objections: (1) there is no structural evidence that the seed-pedicel is a bud, or an axial structure of any kind;[2] (2) neither is there any evidence that the pedicels are axillary to certain of the interseminal scales; (3) there is no known structure among the Cycadophyta or Pteridospermeae from which such an organ as the supposed unifoliar female flower could have been derived by reduction. In an earlier work[3] Professor Lignier supported his interpretation by a comparison with certain fructifications of Cordaiteae, in some of which, as already mentioned, the seeds were borne at the ends of long peduncles. The analogy, however, is of little value, for the two families are so far apart that their common origin was probably too remote to have led to any community of floral characters. On the whole, the axial theory of the seed-pedicels, though supported with much ingenuity, appears, so far as our present knowledge shows, to lack an adequate structural or comparative basis.

On the alternative hypothesis, all the organs constituting the gynæcium are of the nature of leaves, and borne, in accordance with the observed facts, directly on the axis. Dr. Wieland regards as most tenable "the theory that the seed-pedicel and the

[1] O. Lignier, "Le fruit des Bennettitées et l'ascendance des Angiospermes," *Bull. Soc. Bot. de France*, ser. iv. t. viii. 1908.

[2] Unless it be found in the somewhat deeper insertion of the interseminal scales, as compared with the pedicels—a very dubious indication. See Wieland, *l.c.* p. 118.

[3] *Structure et affinités du Bennettites Morierei*, 1894, pp. 68 and 72.

interseminal scale are greatly reduced sporophylls analogous to and derived from sporophylls like those of the existing Cycads."[1] Arber and Parkin, who likewise regard the whole fructification as a flower, or "anthostrobilus," to use their own term,[2] consider that the interseminal scales are "homologous with the carpels of the Angiosperms, despite the fact that they subtend and do not bear the seed-pedicels."[3] They point out "a possibility that the seed-pedicels may, in part, represent a lobe of the carpellary leaf,"[4] and that they may or may not be homologous with the funicle of Angiospermous seeds.[5] Professor Lignier argues with considerable force against the suggestion that seed-pedicels and interseminal scales represent lobes of the carpellary leaves, pointing out the complete independence of the bundles supplying the two organs, the absence of any definite relation in their arrangement, the differences in their structure, and especially the fact that in *Bennettites Morierei* the outer interseminal scales have several vascular bundles and are flattened like the bracts.[6] It seems better to take the view that the interseminal scales are, like the bracts, modified leaves, though much more reduced, while we regard the seed-pedicels as the reduced megasporophylls or carpels. The interseminal scales *may* be sterile

[1] *L.c.* p. 231.

[2] They apply the term "pro-anthostrobilus," to the Bennettitean flower, to indicate its primitive features.

[3] *Origin of Angiosperms*, p. 59.

[4] *L.c.* p. 66.

[5] *L.c.* p. 65.

[6] O. Lignier, *Le fruit des Bennettitées*, 1908, p. 7; "Notes complémentaires sur la structure du *Bennettites Morierei*," *Bull. de la Soc. Linn. de Normandie*, sér. v. vol. xiii. 1904. I have occasionally observed interseminal scales with two bundles in *Bennettites Gibsonianus*.

carpels, but there seems to be no reason for assuming this, and the transitional forms between scales and bracts are against it. On the view here provisionally adopted, the whole lateral axis constituting the flower may be compared to the main axis of a *Cycas*, or rather to that of a hypothetical Cycadophyte or Pteridosperm bearing both male and female sporophylls, the leaves adjacent to the sporophylls being reduced, as are the scale-leaves of *Cycas*. The bracts are but little modified, while the stamens fully retain their foliar characters, and have been well compared by Wieland to the megasporophylls of *Cycas*. The interseminal scales and the monospermic carpels have undergone a somewhat extreme reduction, and their arrangement appears very different from that of the whorled stamens, though a verticillate order may possibly yet be traced in the organs of the gynæcium. The reduction demanded by the carpellary theory is, of course, far less than that which the axial theory of the pedicel requires ; on the latter view each monospermic pedicel would be the homologue, not merely of a carpel, but of an entire strobilus.

As compared with the seed of a Pteridosperm or Cycad, that of the Bennettiteæ is considerably simplified, especially in its vascular system, which appears to be almost limited to the chalazal disc or socket. This reduction is no doubt correlated with the enclosure of the seeds in a fruit.

Our knowledge of the earlier Cycadophyta is at present quite insufficient to enable us to form any conception of the course of evolution of the Bennettitean flower. The discovery of Triassic Cycadophytes

with structure preserved would be likely to throw some light on the question. Unfortunately our accurate knowledge of the structure of these plants in Mesozoic times, though of extraordinary interest and value, is still limited to a comparatively narrow group—a special family which had attained a leading position in those days, somewhat as the Compositae have in the recent Flora. The Williamsonias diverge widely, in habit, from the usual Bennettitean type, but in their case we have as yet no knowledge of the internal structure.

The discovery of the bisexual nature of the flower and the arrangement of its parts has so greatly strengthened the Angiospermous analogies of the Bennettiteae, that an actual, though not a direct relationship, now appears probable. This important subject, however, will be left for discussion in the concluding chapter.

As regards affinities in other directions, the relation to the Cycadaceae is universally recognised, and has been sufficiently dwelt on above. Further research will be necessary before we can hope to determine the common ancestry of the two lines, with which other Cycadophytic phyla, as yet unknown, may have converged.

Advanced as the Bennettiteae were in their floral organisation, there can be no doubt that they were still Gymnosperms as regards their mode of fertilisation, as shown by the fact that the micropyles were exposed, protruding through the openings left between the coherent scales of the pericarp.

The stamens, while in their arrangement and monadelphous fusion they suggest the androecium of

a fairly advanced Angiosperm, in structure and form correspond to the sporophylls of a Fern, their compound pollen-sacs, or synangia, exactly recalling those of some recent Marattiaceae. It is, however, improbable that these Fern-like characters (among which the ramenta must also be reckoned) came to the Bennettititeae directly from any group of true Ferns. There can be little doubt that the Bennettititeae and the Cycadophyta generally trace their descent through the Pteridosperms, and that it is by their means that the Filicinean features, so conspicuous in the microsporophylls, have been handed on to the later group; the presence of synangia, in particular, can thus be explained. It is certainly a striking fact that this family, so highly advanced in general floral structure and in the characters of the gynæcium, should have retained, with so little modification, a form of microsporophyll which is essentially that of a Fern.

The Bennettititeae thus present an extraordinary combination of characters, Filicinean, Gymnospermous, and Angiospermous. Their investigation, as we shall see in the next chapter, has for the first time thrown light on the great and obscure problem of the descent of the higher Flowering Plants.

II. Coniferae

The question of the origin and early history of the Coniferae, now the predominant Order of Gymnosperms, is clearly one of the most important on which fossil botany may be expected to throw light. At present, however, the evidence on these points is

imperfect, so that Coniferous remains, though abundant enough, have been spoken of as among the most unsatisfactory objects with which the palæobotanist has to deal. Of late years some real advance has been made, but the Coniferae are still, in the present state of our knowledge, unsuited for full treatment in the present course, the object of which is to bring forward only the best-ascertained results in our subject. One or two points, however, may be briefly referred to.

The Coniferae are evidently of great antiquity, for remains which can only be referred to this Order have been found with certainty in the Permian and possibly in earlier Palæozoic strata. An interesting Permian genus, unfortunately still imperfectly known, is *Walchia*, leafy twigs of which are common fossils, while some specimens have been found in fruit. The habit of these branches, of which several species have been described, is quite like that of some of the recent *Araucarias*, such as the Norfolk Island Pine, *A. excelsa*. Certain curious fossils, long described as a distinct genus, under the name of *Tylodendron* or *Schizodendron*, have turned out to be casts of the medullary cavity of stems, probably identical with those of *Walchia*, to which they would thus stand in precisely the same relation as that of the *Sternbergia* casts to the stem of *Cordaites*. The casts are marked with a characteristic areolation, corresponding to the course of the primary vascular bundles, and agree wonderfully closely with the configuration of the pith in the recent genus *Araucaria*. The structure of the wood, surrounding the pith of *Tylodendron*, is sometimes preserved, and is found to be of an *Araucarioxylon* type, known as

A. Rhodeanum, differing from the Cordaitean wood in the arrangement of the pits and some other trivial characters.

Unfortunately, our knowledge of the *Walchia* fructifications does not go much beyond their external features. On certain specimens, small scaly cones are borne, some of which were probably male, while others are known to have been female; in *Walchia filiciformis*, Zeiller[1] showed that each scale of the female cone bore a single seed, an important Araucarian character. In a specimen described by Renault, on the other hand, the lateral twigs each terminate in a bud-like body apparently containing a solitary seed[2] (*Walchia frondosa*, Ren.). On the evidence available there appears to be some ground for referring such a species as *W. filiciformis* to the Araucarieae, the essential character of which lies in their fructification, and especially in the carpellary scales, each of which in the recent members of the family bears one ovule directly, without the intervention of a seminiferous scale. In vegetative characters there is also considerable agreement, but it appears most probable that under the name *Walchia* very distinct types have been confounded. It has been maintained that Araucarieae are the oldest tribe of Coniferae; this statement, in the first instance, no doubt depended largely on confusion between Cordaiteae and Araucarieae; the former group is now excluded from the question, but there is some evidence, as we have seen,

[1] *Bassin houiller et permien de brive flore fossile*, 1892, p. 99, Plate xv.

[2] Renault, *Flore fossile d'Autun et d'Epinac*, Part ii. p. 357, Plate lxxviii. See also Potonié, *Lehrbuch der Pflanzenpalaeontologie*, 1899, p. 292, for a general account of *Walchia*.

that, in the Permian period, Conifers resembling Araucarieae both in vegetative and reproductive characters already existed.

The evidence for the antiquity of the Araucarieae has recently been summed up by Professor Seward.[1] In Triassic, Rhætic, and Liassic beds there are a number of specimens of twigs, wood, and cones which may probably be Araucarian, but none appear to be absolutely decisive. From the Jurassic onwards the evidence, from well-preserved cones and other remains, is ample and convincing. It is interesting to find that examples of probable Araucarieae with more than one seed on the carpellary scale have recently been described from Cretaceous horizons. In the genus *Protodammara*, of Hollick and Jeffrey, from the State of New York, there are three seeds on each scale, while the anatomical structure indicates a relation to the recent genus *Agathis*.[2] In the *Pseudoaraucaria* of Fliche, from the Albian of the Argonne, each scale bears two seeds, and the structure suggests a possible link between the Araucarieae and Abietineae.

The Taxodieae, the tribe to which the famous "Big Trees" of California (*Sequoia gigantea*) belong, may claim a high antiquity, if the genus *Voltzia*, from the Upper Permian and Triassic, is rightly referred to this group. The evidence in this case does not depend merely on vegetative characters, but is strengthened by the morphology of the cone, the

[1] Seward and Ford, "The Araucarieae, Recent and Extinct," *Phil. Trans. Royal Soc.* B, vol. 198, 1906, p. 370.

[2] A. Hollick and E. C. Jeffrey, "Affinities of Cretaceous Plant Remains commonly referred to *Dammara* and *Brachyphyllum*," *American Naturalist*, vol. xl. 1906.

seminiferous scales of which are lobed, as in the recent genus *Cryptomeria*. *Voltzia*, however, has also been regarded as an Araucarian. A number of other fossil remains have been referred to the Taxodieae, but they are for the most part of Tertiary or Cretaceous age. Cones closely resembling those of *Sequoia*, attached to leafy branches of the type known as *Brachyphyllum*, have, however, been found by Professor Zeiller in the Lias of Madagascar.

As regards remains of the Abietineae, the fossil cones are seldom well enough preserved to show the seeds in relation to the seminiferous scale, the character on which the identification of the tribe depends; in the case of such a genus as *Pinus*, however, the grouping of the needles on short twigs is so characteristic as to leave little doubt of the affinity, when this feature is associated with a resemblance in the habit of the cones. It has been known for some time that Abietineae, allied to *Pinus*, occurred in the Wealden formation; the evidence is strengthened by the occurrence of Abietineous wood at the same horizon.[1] Recently the genus *Pinus* has been recognised, on the evidence of characteristic cones, in the Portlandian (Upper Oolite), while Abietinean wood has also been found in deposits of Jurassic age. Professor Jeffrey has lately described, under the name of *Prepinus*, leaves of a Cretaceous Conifer, preserved as lignite, which, while showing clear indications of affinity with *Pinus*, possess centripetal xylem in the bundle, and other primitive characters, even recalling the structure of

[1] Seward, "Plants of the Wealden," Part ii. p. 193; "On a New Species of Conifer, *Pinites Ruffordi*," *Journal of the Linnean Society*, vol. xxxii. p. 417, 1896.

Cordaitean leaves to some points. He regards *Prepinus* as a probable ancestor of the true Pines.[1]

Fossils from beds of much greater age—the Rhætic, for example (*Schizolepis*)—have been referred to Abietineae, but the evidence does not seem to be decisive.

Cupressineae have not been traced with certainty very far back, though twigs and cones of Cupressineous habit occur in the Jurassic. A fossil species of the recent genus *Callitris* (*Widdringtonia*) has been described from the Upper Cretaceous of Moravia, and seems to be an extraordinarily clear specimen, with characteristic cones of both sexes well preserved.[2] If a recent genus already existed, in a characteristic form, in Cretaceous times, it is certain that the group to which it belongs must have been of very considerable antiquity, but we can only look to future discoveries for further light on its history.

The Taxaceae, as now limited (exclusive of *Ginkgo*), have not been traced back with certainty to a lower horizon than the Cretaceous, though branches with leaves like those of the genera *Cephalotaxus* and *Podocarpus* have been described from the Potomac formation, probably of about Wealden age. Professor Nathorst[3] has quite recently shown that his genus

[1] E. C. Jeffrey, "On the Structure of the Leaf in Cretaceous Pines," *Ann. of Bot.* vol. xxii. 1908.

[2] Potonié, *l.c.* p. 317, Fig. 322. The student will find an excellent summary of the geological history of the Coniferae in Professor Potonié's text-book. For the more recent work on the subject see Zeiller, "Les Progrès de la paléobotanique de l'ere des gymnospermes," *Progressus Rei Botanicae*, Bd. ii. 1907.

[3] "Paläobotanische Mitteilungen. 7. Ueber *Palissya*, *Stachyotaxus*, und *Palaeotaxus*," *Kongl. Svenska Vetenskap Akad. Handl.* Band xliii. No. 8, Dec. 1908.

Stachyotaxus, of Rhætic age, has much in common with *Dacrydium*, though in the fossil there are two seeds to each carpellary scale, instead of one. He further suggests the possibility that the contemporary *Palissya*, with five or six pairs of seeds on each carpel, may be related, though he points out as an alternative view that these genera may belong to an extinct race of Gymnosperms, intermediate between Coniferae and Cycadophyta.

Coniferous wood, in a petrified, and especially in a silicified condition, is among the commonest fossils of the Mesozoic strata. Such specimens, for example, are most abundant in the Lower Greensand and Wealden of the Isle of Wight, and in the Purbeck beds of Eastern Dorsetshire. Often, the preservation is absolutely perfect, so that the finest details of histological structure can be studied.[1] Yet the results of such investigations have so far been on the whole unsatisfactory, and, however elaborately carried out, have rarely, as yet, enabled us to determine with any certainty the particular family to which a given Coniferous specimen belonged. The recent investigations of Dr. Gothan,[2] however, in which additional characters, and especially the details of structure of the medullary rays, are taken into account, give promise of more definite results.

The study of the fossil Coniferae is not yet sufficiently far advanced for us to decide which of their

[1] See Barber, "*Cupressinoxylon vectense*," for an especially careful and detailed examination of a Mesozoic Coniferous wood, *Annals of Botany*, vol. xii. 1898.

[2] See W. Gothan, "Zur Anatomie lebender und fossiler Gymnospermen Hölzer," *Abhandl. der k. Preuss. Geol. Landesanstalt*, Heft 44, 1905.

families is the most ancient, or to form any clear conception of the course of their evolution. The direct palæontological evidence, however, apart from theoretical considerations, is favourable to the opinion that the Araucarieae have the longest fossil history, probably overlapping that of the typically Palæozoic Order Cordaiteae.

The discovery of fresh sources of evidence from remains with structure preserved, as in the case of the Cretaceous lignites of the eastern United States, now under investigation by Professor Jeffrey and his colleagues, is likely to throw much new light on the geological record of the Coniferae.

III. Ginkgoaceae

That isolated type, the genus *Ginkgo*, now regarded as constituting an Order, or even Class, by itself, has proved to be of great antiquity. Here we have to do with a well-characterised, easily recognised group, and the palæontological evidence is consequently of great significance.

The habit of the leaves of *Ginkgo* is so characteristic, that the evidence from fossil leaves, agreeing in form and venation with those of the recent genus, is in itself of some value. Such leaves have been recorded in abundance, from the Coal-measures onwards, and though many are doubtful, and may probably have belonged to Ferns, resembling in their foliage *Actinopteris*, or certain species of *Schizaea*, others are in all probability rightly attributed to the Ginkgoaceae. The genus *Whittleseya*, from the Lower Carboniferous, with

leaves differing from those of *Ginkgo* in their short petioles and other characters, appears to be connected with the typical form by the new genus *Ginkgodium*, from the Lower Oolite of Japan. The genus *Baiera* of Braun is the most important group, and is distinguished from the recent *Ginkgo* by possessing a lamina with more numerous and narrower segments. This distinction, however, has no constant value, as some forms of leaf, even in the recent species, are much more deeply dissected than others. "The genus," says Mr. Seward, "was probably most widely spread during the Jurassic period, but there is fairly strong evidence in favour of extending its range to the Palæozoic epoch."[1] Many of the Triassic and Jurassic leaves are referred to the genus *Ginkgo* itself, and some are even indistinguishable from those of the recent Maidenhair tree, or can only be distinguished by the microscopic characters of the epidermis and stomata, points which have now been investigated with much success in carbonised specimens.

The evidence from the leaves is supported by the discovery of specimens of flowers and seeds, which appear to be conclusive as to the existence of the Ginkgoaceae, at least in Mesozoic times. As regards the Palæozoic evidence, Mr. Seward is of the opinion that "the plants which possessed characters nearest akin to those of *Ginkgo* were probably members of the Cordaitales, an extinct stock with which the Ginkgoaceae are closely connected" (*l.c.* p. 142).

In the Jurassic beds of Siberia, male flowers, agree-

[1] Seward and Gowan, "The Maidenhair Tree (*Ginkgo biloba*, L.)," *Annals of Botany*, vol. xiv. March 1900. See also A. Sprecher, Le *Ginkgo biloba*, Geneva, 1907.

ing closely with those of the recent species, have been found, associated with the *Ginkgo* leaves, and similar specimens have been described from the Inferior Oolite of Yorkshire.[1] Male flowers, found in Germany at a lower horizon, on the boundary of the Trias and Lias, were associated with *Baiera* leaves, and differed from the flowers of *Ginkgo* in the greater number of pollen-sacs borne on each stamen. This point is of interest, in view of the comparison with the male flower of Cordaiteae suggested above (Chapter XII. p. 538). Female flowers and seeds have also been discovered, but as the seeds are usually detached, the evidence is not quite so satisfactory on this side. Prof. Seward's views as to the Ginkgoaceous affinities of *Beania* have already been mentioned (p. 595). In this case, however, the reasons for connecting the flower with Cycadaceae seem about equally strong.

On the whole, the sum of the fossil evidence is of sufficient weight to prove the great antiquity of the Gymnospermous family now represented by the Maidenhair tree, which appears to be best regarded as the one surviving member of an ancient stock, derived from the same cycle of affinity as the Palæozoic Cordaiteae, once the dominant type of Gymnosperms.

[1] A. C. Seward, *Jurassic Flora*, Part i., 1900, p. 260.

CHAPTER XIV

GENERAL RESULTS

THE first broad conclusion arrived at from the study of fossil botany—the great relative antiquity of the Vascular Cryptogams and Gymnosperms, as compared with the Angiospermous Flowering Plants—still holds good, though we should now state this fundamental generalisation in rather different terms from those used by its original author, the great Brongniart.[1] The lower Seed-plants were more prominent in Palæozoic times than Brongniart was aware, and differently constituted, for while his Asterophylliteae and Sigillarieae[2] have proved to be Cryptogamic families, the ranks of the Spermophyta have received a more than equivalent accession in the Pteridosperms, now transferred to them from the Ferns. Brongniart's conclusion was far from being an obvious one at the time, for he and his contemporaries still included the Gymnosperms under Dicotyledons, so that in recognising the much higher antiquity of the former the palæontologist anticipated the results of the comparative morphologist.

[1] See his "Tableau des genres de végétaux fossiles," p. 93, *Dictionnaire universel d'histoire naturelle*, 1849.

[2] *L.c.* p. 97.

The question of the classification of the groups of plants with which we have been concerned may be considered here, before going on to the results under each group. To a considerable extent the question turns on the position of the Sphenophyllales; we have recognised that they form a synthetic group, and have dwelt especially on their apparent relations to the Equisetales and the Lycopods, suggesting the common origin of these phyla. As regards the relation between the Sphenophyllales and the Equisetales there is little room for doubt, as will be shown below (p. 619); this may be expressed by grouping together the two classes under the name Articulatae, in accordance with a suggestion of Professor Lignier's, and adding the new group Pseudoborniales. The same author regards both Sphenophyllales and Equisetales as derived from primitive Ferns,[1] and although I am not able to follow all his arguments in detail, I think there is some evidence of affinity in this direction. The Sphenophylls resemble certain Ferns in the venation and frequent dichotomous division of their leaves; they are not really microphyllous like the Lycopods. The oldest Equisetales likewise had forked leaves, while in the Devonian Pseudoborniales, which clearly belonged to the Articulatae, the leaves were highly compound. So far as the leaf-characters are concerned, the Lycopods appear to stand alone as the one truly microphyllous phylum. On the other hand, the Sphenophylls certainly approach the Lycopods in their anatomy, though the taxonomic

[1] O. Lignier, "Equisétales et Sphénophyllales, leur origine filicinéenne commune," *Bull. Soc. Linn. de Normandie*, 5e sér. 7e vol. p. 93, Caen, 1903; "Sur l'origine des Sphénophyllées," *Bull. Soc. Bot. de France*, sér. 4, tome viii. p. 278, 1908.

value of the characters which they have in common is difficult to estimate. In some respects the Psilotaceae seem to connect the Sphenophylls with the Lycopods, but it is not wise to rely much on evidence from a recent family in questions of remote ancestry. Although various attempts have been made to group all the classes of vascular plants under two main heads, it seems that in the present state of our knowledge a threefold division is still to be preferred, so as to avoid prejudicing questions which are still open.

The affinities of the Equisetales, Pseudoborniales, and Sphenophyllales are generally admitted; to them we may append the Psilotales, for reasons which will be subsequently explained (p. 626). The Lycopodiales are at present best left by themselves, for the fossil members show little or no approximation to any other phylum.

The Ferns likewise appear to have followed their own course of development from the earliest times to which our records extend; they show, however, evident affinities with the great bulk, at any rate, of the Seed-plants. Our provisional arrangement may, therefore, take the following form:—

Sphenopsida	Equisetales Pseudoborniales Sphenophyllales Psilotales	*Articulatae.*
Lycopsida	Lycopodiales	
Pteropsida	Filicales Pteridospermeae Gymnospermeae Angiospermeae	*Spermophyta.*

It will be noticed that this grouping crosses the customary division of Vasculares into Pteridophyta and Spermophyta. Though the traditional classification will, no doubt, continue to be used on grounds of convenience,[1] it no longer, in the light of the palæobotanical evidence, expresses a natural arrangement, for the affinities between Pteridosperms and Ferns appear to be far closer than those between Ferns and any other Pteridophytic phylum.

The divisional name Pteropsida is taken from Professor Jeffrey, and used in the same sense as by him. His Lycopsida, however, are here limited to the Lycopodiales, the typically microphyllous phylum, while he included our Sphenopsida in the same division. This is not the place for a detailed discussion, but I am no longer of opinion that the affinity between Lycopods and the sporangiophoric Pteridophytes (Professor Bower's name for our Sphenopsida[2]) is sufficiently established to render their inclusion under a common name expedient. The name Sphenopsida has been selected because of the synthetic character of the class Sphenophyllales, rendering them the best type of the division.

A certain degree of convergence between the main divisions of Vascular Plants may be traced as we follow their history back to its earliest records. Some of the oldest Sphenopsida show an approach in leaf-characters to the megaphyllous Fern-phylum, while anatomically they tend rather towards the

[1] As in the subtitles given to the two volumes of the present book.

[2] F. O. Bower, *Origin of a Land Flora*, 1908, Chapters xxvii.-xxix. The author's association of the classes with specialised sporangiophores appears eminently natural and suggested the arrangement here adopted.

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Lycopods. The record does not go far enough back to show whether this convergence really indicates a common origin for all Pteridophyta from a single stock; though such an hypothesis is quite tenable.

The question of the ancestry of the Vasculares or of the origin of their characteristic alternation of generations is not as yet directly touched by the palæontological evidence. The general character of the earliest known land-floras, however, and especially the prevalence of megaphyllous types, lends no support to the idea that the spore-bearing plant of the Pteridophytes was ever derived from a sporogonium, whether Bryophytic or otherwise. On the other hand, the evidence, so far as it goes, is perfectly consistent with the hypothesis of the origin of the sporophyte from a branched thallus, a view which has gained ground of late years.[1]

As regards the difficult question of the relation of the Pteridophyta to the Bryophyta, we have no positive evidence from fossil botany, for scarcely anything is known of the history of Bryophytes. One or two supposed Liverworts and Mosses have been recorded from Palæozoic rocks, but in the absence of any knowledge of their structure or reproduction the nature of the specimens must remain doubtful. It is remarkable that no remains of Bryophyta have been detected in the petrified material, in which the most

[1] See A. G. Tansley, "Evolution of the Filicinean Vascular System," *New Phytologist* Reprint, 1908, Lecture I.; W. H. Lang, "A Theory of Alternation of Generations, based upon Ontogeny," *New Phytologist*, January 1909. The antithetic view, on the other hand, forms the basis of Professor F. O. Bower's work, *The Origin of a Land Flora*, 1908. The present position of the question is illustrated by a discussion at the Linnean Society, reported in the *New Phytologist* for 1909.

delicate tissues are preserved and a great variety of organisms represented. The question of the existence of Palæozoic Bryophyta must still be regarded as an open one. The hypothesis that the Pteridophyta arose from a Bryophytic ancestry has thus received no support from the palæontological record.

We will now go on to consider, somewhat more fully, the affinities of the various groups of Vascular Plants dealt with, beginning with the articulated Sphenopsida.

Sphenopsida

The general morphological agreement between the two classes Sphenophyllales and Equisetales is manifest, and extends to Nathorst's new class Pseudoborniales. The articulated stem, and the constant verticillate arrangement of the appendages, are characters obviously common to the whole series. *Archaeocalamites*, the oldest of the known Equisetales, distinctly approaches the Sphenophyllales in the superposition of the verticils and in the dichotomously divided leaves, while in many Calamariaceae the individual leaves resemble the leaves or leaf-segments of the plurifoliate Sphenophyllums so closely as to be almost indistinguishable. Professor Lignier has endeavoured to carry the comparison further and to place it on an anatomical basis. In the typical species of *Sphenophyllum* there are six leaves in a whorl, but the vascular strands supplying each two leaves start from the same angle of the triarch stele, suggesting that three was the original number of leaves in a verticil. In some

species (e.g. *Sphenophyllum Dawsoni*, p. 101) the increased number of leaves has affected the stele itself, each of its angles being double. When the leaves are further segmented, a further forking of the bundles takes place within the cortex, and it appears indisputable that the numerous leaves of such a species as *S. myriophyllum* represent the segments of a few deeply divided original appendages. In the Calamariaceae, on Lignier's view, the same process has gone further, the increased dimensions of the stem involving a corresponding multiplication of the leaves and of the bundles in the stem. In cases like the axis of *Calamostachys*, we have a clear analogy with *Sphenophyllum* in the fact that each two bracts receive their vascular supply from the same axial bundle, while in *Palaeostachya vera* the axial bundles are themselves duplicated, forming evident pairs (p. 65). It certainly appears highly probable that the small and numerous whorled leaves of the Calamariaceae may have arisen, as in the Sphenophyllales, by the subdivision of a smaller number, with corresponding anatomical changes. That the leaves were originally compound or much cut is rendered probable by the presence of such divided leaves in the early fossils *Archaeocalamites*, and more especially *Pseudobornia*, the leaves of which, when found isolated, were actually taken for the fronds of a Fern.

In anatomy, the Sphenophyllales, with their solid protostele, appear to be clearly more primitive than the Equisetales, which in all cases have a pith and distinct vascular bundles. The anatomical gap between the two classes appeared a very wide one, until it was partly bridged by the discovery of centripetal wood in

the stem of the Lower Carboniferous *Protocalamites* (p. 37).[1]

The evidence from the fructifications strongly supports the affinity between Sphenophyllales and Equisetales, though the detailed comparison presents some difficulties. The minute structure of the sporangia is strikingly similar in the two classes, and the resemblance extends to the sporangiophores. Those of *Cheirostrobus* in particular, which have four sporangia, are almost identical with those of *Calamostachys* (pp. 54 and 116). Where the number of sporangia is smaller the resemblance to the Equisetal type becomes less evident.

Throughout the Sphenophyllales the sporangiophores occupy the position of ventral lobes of the sporophyll; in one species, *S. fertile* (p. 111), the dorsal lobes are also enlisted for the same service. This latter case is of special interest, because the dorsal and ventral lobes are on an equal footing, both being organised in the same way; the segments of each lobe constitute typical bisporangiate sporangiophores. I incline to regard this form as a secondary modification rather than a primitive type, partly because the case is at present altogether exceptional and of no special antiquity, and partly because the dorsiventral arrangement seems best explained on the supposition that the dorsal lobes were originally sterile and protective

[1] Mr. Gwynne-Vaughan has suggested that the lateral xylem-strands in the recent *Equisetum* may represent the centripetal wood. Their position, however, is very different from that of the centripetal wood in *Protocalamites*, and the matter requires further investigation. See D. T. Gwynne-Vaughan, "Remarks upon the Nature of the Stele of *Equisetum*," *Ann. of Bot.* vol. xv. 1901, p. 774.

in function. It may be added that the very leaf-like character of the bracts in most Sphenophylls, and especially in *Sph. majus* (p. 113), makes it difficult to interpret them as sterilised sporangiophores. But whether we regard *S. fertile* as a modified or a primitive form,[1] it shows clearly that the sporangiophores and bracts have equal claims to be regarded as lobes of the sporophyll. This conclusion applies also to *Cheirostrobus*; it is only in *Sphenophyllum emarginatum* that the sporangiophores and bracts appear to have been independent, as they have left separate scars on the axis of the cone.[2]

In *Calamostachys*, among the Equisetales, the two organs are externally quite separate, but the course of the bundles supplying the sporangiophores suggests that the latter may represent displaced ventral appendages of the bracts (p. 60). *Palaeostachya*, from the position of the sporangiophores immediately above the bracts (p. 66), seemed at first to form a link with the Sphenophyllales, but Mr. Hickling's observations on the vascular supply rather suggest a modification of the *Calamostachys* arrangement. The *Equisetum* type of strobilus appears to have been already represented in Palæozoic times, and in *Archaeocalamites* the bract-whorls were, at most, few and scattered. It has been proposed to derive the bractless arrangement from that found in *Sphenophyllum fertile*, the assumption being that the lobes of a wholly fertile sporophyll underwent a displacement like that which appears to

[1] The latter view is maintained by Lady Isabel Browne in her interesting résumé of the "Phylogeny and Inter-relationships of the Pteridophyta," *New Phytologist*, vol. vii. 1908, p. 94.

[2] As shown by an unpublished observation of Mr. W. Hemingway's.

have taken place between the sterile and fertile lobes in *Calamostachys*.[1] The evidence, however, is as yet insufficient to establish any such interpretation, and it may well be that the *Sphenophyllum* analogy has been pushed too far. There is no need to reduce every sporangiophore to a leaf-lobe, for it is not at all unlikely that in the Sphenopsida, as in the Pteropsida, the spore-bearing organ may be sometimes a lobe of a leaf, sometimes an entire leaf, especially as it is often so difficult to distinguish between leaf-segments and leaves in the vegetative region.

Professor Bower regards the sporangiophore as "a part *sui generis* as much as the sporangium is, and not the result of modification of any other part."[2] Miss Benson, from a different point of view, has been led to a similar conclusion.[3] There is much to be said for this interpretation, which I provisionally adopted in the First Edition of these "Studies" (p. 498). On the actual evidence, however, there is nothing to prevent our regarding the sporangiophore as always of a foliar nature, and it appears unadvisable to multiply categories of organs without necessity. The sporangium and the sporangiophore are not really on the same footing, for there must always have been distinct organs of reproduction, whereas in innumerable cases the organ which bears them is simply a leaf, or part of a leaf. At the same time it is probable that the differentiation of the sporangiophore took place very early,

[1] Scott, "Present Position of Palæozoic Botany," *Progressus Rei Botanicae*, Bd. i. p. 162, 1906.

[2] *Origin of a Land Flora*, p. 426.

[3] "The Sporangiophore—a Unit of Structure in the Pteridophyta," *New Phytologist*, vol. vii. 1908, p. 143.

in certain lines of descent, and that the organ is thus of considerable morphological importance.

On the whole of the evidence there can be no doubt that a real affinity exists between the Sphenophyllales and the Equisetales, the former being clearly the more primitive class of the two, or rather the representatives of a more primitive stock, for the known Sphenophylls are evidently specialised in various directions. The arguments for the aquatic habit of *Sphenophyllum* do not hold good, as already pointed out (p. 88); the great development of the wood relatively to the size of the stem is the reverse of what one would expect in a water-plant; on the other hand Professor Seward's suggestion that *Sphenophyllum* may have been "a slender plant which flung itself on the branches and stems of stronger forest trees for support,"[1] agrees well with the habit and structure. The occurrence of extensive secondary growth in this genus is interesting, as showing that this character was not necessarily correlated, even in Palæozoic times, with an arborescent habit.

The enormous development of the Equisetales in early geological periods, compared with their reduced condition at the present day, is a striking fact. It is of interest to consider in what respect the gigantic Palæozoic Horsetails differed from their humbler successors.

One great and obvious difference was the formation of secondary wood and bast and of periderm. Starting with a structure in stem and root essentially like that of a recent *Equisetum*, the Calamariaceae, by the activity of a normal cambium, produced new wood and phloëm,

[1] *Fossil Plants*, vol. i. 1898, p. 392.

to an indefinite extent, precisely as in a Gymnospermous tree, and replaced their primary cortex by a broad zone of secondary periderm. It was one of Williamson's greatest services to science that he always, in the face of much opposition, insisted on the true "exogenous growth" of the Calamites, while maintaining with equal decision their Cryptogamic nature. He thus established one of the most striking instances of homoplastic modification, for the close agreement in these anatomical characters between certain Cryptogams and Phanerogams is not, in itself, any proof of affinity.

As has already been pointed out, it is probable that the microphyllous character is not a primitive one in Equisetales, and that the leaves are reduced from a larger and more complex type, as seen in *Archaeocalamites* and *Pseudobornia.*

The old opinion of the French school that some Calamariaceae were seed-bearing plants has not been substantiated by later work. Heterospory, however, appears in a perfectly well-marked form in some of the fructifications, though the differentiation of the two kinds of spore was not so extreme as in heterosporous Lycopods or the recent Water-ferns. In other Calamarian strobili the evidence is all in favour of homospory; the abortion of certain spores in sporangia of this type may have prepared the way for the heterospory of the more advanced members of the group (p. 57). In this respect the Equisetales seem to have reached a higher level than the Sphenophyllales, among which only doubtful indications of incipient heterospory have so far been detected.

Considering the high development of the Palæozoic

Equisetales, it is an interesting question whether our living Equiseta are their degenerate descendants, or the offspring of a simpler stock which may have co-existed with the arborescent forms in ancient times. The earlier Mesozoic Equisetales appear to have been intermediate in certain respects between the Calamariaceae and the recent genus, as shown especially by Mr. Halle's results (p. 83). By Wealden times, forms almost identical with modern Horsetails had appeared. These facts favour the hypothesis of reduction, which may also be supported by the observation (if rightly interpreted) of secondary growth, at the nodes of some living Equiseta.[1] The Equisetales, as a class, have conspicuously failed to hold their own in the secular struggle for existence, though the survivors are extraordinarily well adapted to particular conditions, and maintain their ground, when once established, with singular obstinacy.

The possibility of a relation between the Sphenopsida and the Lycopsida will be discussed under the latter head, but we have now to consider the reasons for including the recent group Psilotaceae in the same division with the Articulatae. The question concerns us here because it turns entirely on the relations between the recent family and the Palæozoic class Sphenophyllales. The points of comparison of chief importance are the anatomy of the stem and the morphology of the sporophyll. As regards the former, *Psilotum* presents a nearer analogy with *Sphenophyllum* than any other living plant; the resemblance becomes very marked in those branches

[1] Cormack, *Annals of Botany*, vol. vii. 1893, p. 63.

which have a triarch stele with the wood reaching the centre; in other parts of the *Psilotum* stem a resemblance to the stele of *Cheirostrobus* has been traced. Mr. Boodle's discovery that, at the base of the aërial stem and in adjoining parts of the rhizome, a distinct formation of secondary wood takes place in old plants[1] materially strengthens the anatomical analogy. The mesarch structure of *Tmesipteris* finds some slight analogy in that of *Cheirostrobus* (p. 119). Evidence from the anatomy is, however, insufficient by itself, for on anatomical grounds a comparison of the Psilotaceae with recent and fossil Lycopods is also admissible. The morphology of the sporangial apparatus is more significant, and must now be considered.

The nature of the synangium of the Psilotaceae has long been in dispute. In modern times there have been two principal views: (1) that the synangium is borne directly on the subtending leaf, a forked bract, which is thus regarded as a true sporophyll; and (2) that the synangium represents a fertile branch, the first two leaves of which are fused to form the forked bract. On the second view the sporophylls are assumed to be entirely suppressed. Celakovsky, who upheld the first of these opinions, interpreted the synangium as a fertile, ventral lobe of the sporophyll, comparable to the spike of *Ophioglossum*, and this comparison was adopted by Bower, who regarded the synangium or fertile spike in both cases as ultimately derived from a sporangium which had become septate.[2]

[1] L. A. Boodle, "On the Occurrence of Secondary Xylem in *Psilotum*," *Ann. of Bot.* vol. xviii. 1904, p. 505.

[2] For the most recent statement of Professor Bower's views, see his *Origin of a Land Flora*, 1908, Chapters xxviii. and xxxi.

The comparison with *Ophioglossum* was also emphasized by Mettenius and Solms-Laubach, and from a purely morphological point of view appears to be well justified. The groups Psilotaceae and Ophioglossaceae are, however, so widely divergent in their other characters, that any affinity between them must be remote in the extreme. In the Sphenophyllales, on the other hand, we have a group, with which, as we have seen, the Psilotaceae have other characters in common. In the Sphenophylls the sporangia are borne on a ventral outgrowth of the bract or sporophyll, each fertile outgrowth having its own vascular supply, arising as a branch-strand from the bundle of the dorsal bract. In *Tmesipteris* (the less reduced of the two genera of Psilotaceae) the agreement with *Sphenophyllum* is clear. A leaf-trace passes out from the stele and enters the base of the sporophyll, where it divides into three (Fig. 213, B). Two of the branch-strands enter the two forks of the sporophyll, while the third turns upwards, passes through the pedicel of the synangium, and extends into the septum between its two constituent sporangia[1] (Fig. 213, A). Thus the position of the pedicellate synangium and its anatomical relation to the subtending sporophyll correspond exactly to the conditions in the Sphenophyllales. The comparison, originally pointed out in my paper on *Cheirostrobus* in 1897, and further emphasised in the first edition of these "Studies" (p. 499), has received valuable support from the observations of Professor Thomas,[2] of Auckland, New Zealand, who has

[1] For some more detailed observations see below, p. 631.

[2] A. P. W. Thomas, "The Affinity of *Tmesipteris* with the Sphenophyllales," *Proc. Royal Society*, vol. lxix. 1902, p. 343.

had specially favourable opportunities for the investigation of *Tmesipteris* under natural conditions. He has

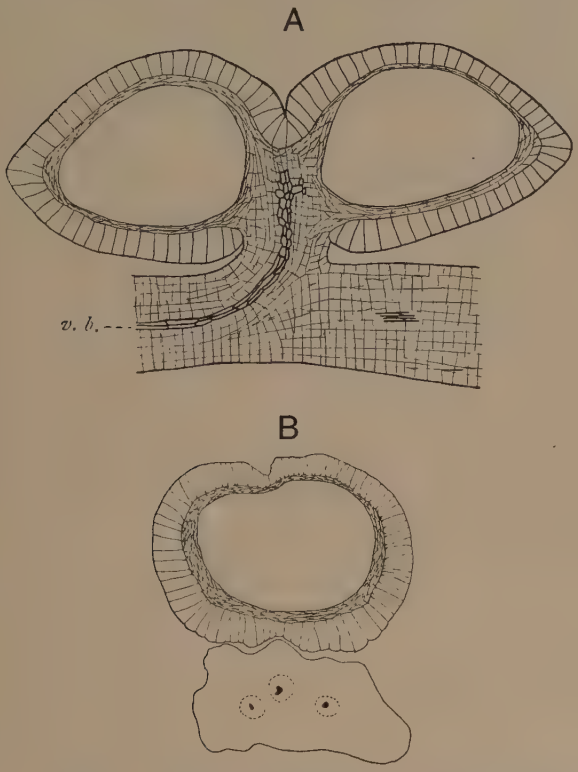

FIG. 213.—*Tmesipteris*. A. Somewhat diagrammatic radial section of synangium and part of sporophyll, showing vascular bundle, *v.b.*, passing into sporangiophore from sporophyll; on the right a fragment of one of the bundles of the forked sporophyll is shown.

B. Transverse section of synangium and sporophyll in a plane lying between the sporangiophore and the stem. In the sporophyll three bundles are shown, the middle strand belonging to the sporangiophore and the two laterals to the forked sporophyll.

found that certain interesting variations normally occur in the species. The most important variation consists in the repeated bifurcation of the sporophyll, a synangium

being present at each bifurcation. This variation occurs, in varying degrees, in the middle of the reproductive region of the most vigorous plants, and is extraordinarily frequent, sometimes extending to a majority of the sporophylls on the shoot. Professor Thomas compares the arrangement in these compound sporophylls with that in *Cheirostrobus* (p. 116); a closer parallel may be found in the repeatedly forked sporophylls of *Sphenophyllum majus* (p. 113), with which the agreement appears to be almost exact, except for an unimportant difference as regards the number of sporangia in each group. In other instances observed by Thomas the synangium acquires an elongated stalk, with somewhat pendulous sporangia, as in *Bowmanites Römeri*. Some similar variations were also observed in *Psilotum*. The repeatedly forked form of sporophyll, which appears to be so common as to fall under the head of normal variations, is unfavourable to the idea of any near affinity between Psilotaceae and the Lycopods, while it affords strong evidence for a relationship to the Sphenophyllales. Such a relationship also explains the forked form of the normal sporophyll characteristic of the family. Taking the anatomical characters also into account, there is thus a strong case for an affinity between the Palæozoic Sphenophyllales and the recent family. I do not, however, go so far as Professor Thomas and Professor Bower, who include the Psilotaceae in the class Sphenophyllales. The differences are, in my opinion, too great to allow of so close a union. The most obvious distinction is in the phyllotaxis, which is spiral, or at least alternate, in the Psilotaceae, while it is always verticillate in the Palæozoic Sphenophyllales.

From the great constancy of this character throughout the Articulatae I am inclined to attach considerable importance to it in this case, though in other groups it may be variable. The mode of branching is also very different, dichotomy occurring in the Psilotaceae, while monopodial branching prevails in the Sphenophyllales. For these reasons, among others, it seems best to regard the Psilotaceae as forming a class of their own, the Psilotales, while including them under the main division Sphenopsida.

Miss Sykes, in an interesting memoir on the anatomy and morphology of *Tmesipteris*,[1] adopts the axial theory of the fructification of Psilotales, and extends it to the Sphenophyllales and the Equisetales, regarding the sporangiophore as representing a branch throughout all these groups. She thus accepts the general view of the relationships maintained by Thomas, Bower, and myself, and endeavours to reconcile it with the axial theory of Bertrand, Goebel, and others. In the special case of *Tmesipteris*, the latter theory is supported, among other arguments, by the observation that the vascular strand entering the synangium-pedicel branches into three, the central strand soon terminating, while the two lateral branches run round the periphery of the septum. The axial interpretation might be a tenable one if the Psilotales stood alone, but throughout the Articulatae there appears to be no satisfactory evidence that the sporangiophore is a branch, while there is much in favour of its foliar nature, as has been shown above. The axial theory seems, on present evidence, to rest on too slender a basis.

[1] *Annals of Botany*, vol. xxii. 1908, p. 63.

Professor Lignier,[1] on the other hand, while regarding the synangium as a terminal spikelet, takes the view that the Psilotales are excessively primitive, being the nearest living representatives of his hypothetical pro-Lycopod type, which he supposes to have formed the starting-point of the Vascular Plants. I cannot accept the epiphytic group Psilotales as really primitive, for one of the two genera bears obvious marks of reduction in relation to habitat, while the other shows signs of modification in the same direction, though in a lesser degree. Neither is there any satisfactory geological evidence for the antiquity of the family in its present form.

Lycopsida

On the whole the fossil record as yet throws singularly little light on the origin and affinities of the Lycopodiales. In the first edition of these "Studies" I laid stress on the relation of this class to the Sphenophyllales, and, through them, to the Equisetales. Professor Jeffrey, on independent grounds, united all these classes in his Lycopsida,[2] as a main division of Vascular Plants, while his Pteropsida included all the remaining groups. It now appears probable that the Articulatae were derived from megaphyllous plants, whereas we have at present no evidence that the Lycopods were ever anything but microphyllous, though the possibility of a reduction from large-leaved forms remains open. Further, the Articulatae and Psilotales are "sporangio-

[1] See his two papers cited above, p. 615.

[2] E. C. Jeffrey, "Structure and Development of the Stem in the Pteridophyta and Gymnosperms," *Phil. Trans. Royal Soc.* B, vol. 195, 1902, p. 144; also his earlier papers there cited.

phoric," bearing their sporangia on specialised appendages, whereas throughout the Lycopods we find a single sporangium seated directly on the sporophyll, or in its axil. This simple arrangement may also be due to reduction; the ventral outgrowth of the sporophyll which bears the sporangium in *Spencerites* has been compared to the sporangiophore of Sphenophyllales, and Miss Benson has recently interpreted the sterile tissue of the sporangium in *Mazocarpon* and an allied fructification as representing a sporangiophore. These suggestions are very interesting, but at present too hypothetical for any conclusion as to affinity to be based on them.[1]

In the anatomy there is no doubt a considerable analogy between the Lycopods, especially the Palæozoic types, and the Sphenophyllales. The stelar structure of *Cheirostrobus*, for example, is much like that of a *Lepidodendron* such as *L. selaginoides*, allowing for the fact that the leaf-arrangement is verticillate in the one and spiral in the other. This type of stele,[2] however, may also occur in Ferns (though not characteristic of that class); its wide distribution is one of the facts in favour of an ultimate common origin for all the vascular phyla. On the whole it appears probable that some remote affinity really exists between the Lycopods and the Sphenopsida, but probably no closer than that between the Sphenopsida and the Ferns.

The Lycopods manifestly attained their highest development in Palæozoic times, as regards abundance,

[1] See also Miss M. G. Sykes, "Notes on the Morphology of the Sporangium-bearing Organs of the Lycopodiaceae," *New Phytologist*, vol. vii. 1908, p. 41.

[2] *i.e.* an exarch protostele.

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stature, and organisation, both vegetative and reproductive. In spite of their immense development at that time compared with their very subordinate position at the present day, the Lycopods, as a whole, constitute a very homogeneous class of plants, characterised throughout by a microphyllous habit, an anatomy based on an exarch type of protostele, and a simple relation between sporangium and sporophyll. There is no departure from the first-named character; for though the leaves were often long, they were never large in proportion to the plant, and were always of the simplest form. The double bundle of *Sigillariopsis*, a form of leaf belonging to certain species of the somewhat advanced genus *Sigillaria*, is the only departure from the prevailing simple type of foliar structure (p. 230).

Attention has already (p. 126) been called to the simplicity of the primary anatomical structure of the stem in Palæozoic Lycopods, the one character in which these plants have proved to be more "primitive" than most of their recent allies. A gradual transition may be traced from the protostelic type, through the medullated forms of *Lepidodendron* and the ribbed Sigillarias, to the smooth-barked Sigillarias, in which the ring of wood separates, more or less completely, into distinct bundles (p. 220). It is these last forms which depart most widely from the common Lycopod type, but the change is not a great one, and does not appear to indicate a transition to any form of Gymnospermous stem.

As regards the secondary growth, characteristic of the arborescent Lepidodendreae, there are some peculiarities; the agreement with the normal secondary

thickening of Gymnosperms and Dicotyledons is somewhat less exact in this class than in the Sphenopsida or the Pteridosperms. In some forms (*Lepidophloios fuliginosus*, for example, p. 154) the zone of thickening is extremely irregular, and although in other Lepidodendreae it approaches the normal type more nearly, it is doubtful whether in any case the same cambium remained continuously active throughout. The secondary growth of *Isoëtes* presents some interesting analogies with that of the Lepidodendreae.

The enormous development of the secondary cortical tissue, chiefly phelloderm, is a striking feature of the tree Lycopods, and with this again the growth of the cortex in *Isoëtes* alone presents any analogy, though, at best, only a remote one.

The difficult question of the morphology of *Stigmaria*, the subterranean part of the Lepidodendroid plant, already discussed (p. 259), suggests that the differentiation between "root and shoot" may have been less sharp in this group than in other Vasculares. Similar indications are to be found in the rhizophores of *Selaginella* and the stem-like roots of some Lycopodiums at the present day. A suggestion has recently been made by Professor F. E. Weiss that an analogy for the Stigmarian axes may be found in the protocorm, the rudimentary, somewhat thalloid, stem which is the first product of germination in some species of *Lycopodium*, and appears to be persistent in the tuber of *Phylloglossum*.

It is a curious fact that among the very numerous fructifications that have been investigated, no certain

instance of a homosporous Palæozoic Lycopod has yet been discovered. Wherever the material has allowed of a definite conclusion, two forms of spore, as sharply differentiated as in any recent members of the class, have been found. *Spencerites* is sometimes cited as an exception, but the evidence is inconclusive, and the spores are singularly unlike those of any known homosporous Lycopod[1] (p. 189). The oldest known genus of Lycopods, *Bothrodendron*, was markedly heterosporous, if we may judge from the Coal-measure species. Among the herbaceous as well as the arborescent Lycopods, only heterosporous forms have so far been detected; in some of the former (*Selaginellites primaevus*) there is an exact agreement with the recent *Selaginella* (p. 264).

It is impossible to doubt that homosporous Lycopods existed in Palæozoic times, but the prevalence of higher methods of reproduction shows how far the class had already advanced at the period when our fossil record begins.

Certain Lycopods, as we have seen (p. 193), went beyond mere heterospory, and developed organs closely analogous to true seeds. Of the two genera in which seed-like organs are known, the one, *Lepidocarpon*, clearly belonged to the Lepidodendreae, while the other, *Miadesmia*, appears to have been a small herbaceous plant, perhaps, as Miss Benson has suggested,

[1] Professor W. H. Lang has recently traced some analogies between the structure of the cone of *Spencerites* and that of *Lycopodium cernuum*. These resemblances, even if fully confirmed, cannot, however, be accepted as indicating affinity until the comparison rests on a much broader basis. See Lang, "Preliminary Statement on the Morphology of the Cone of *Lycopodium cernuum* and its Bearing on the Affinities of *Spencerites*," *Proc. Royal Soc. of Edinburgh*, vol. xxviii. Part v. 1908.

epiphytic on the larger Lycopods with which it is associated. The affinities of *Miadesmia*, which in some respects resembles a *Selaginella*, are not yet determined, but in any case it seems clear that this genus acquired the seed habit on its own lines, and independently of *Lepidocarpon*.

The seed-like organs of these Lycopods, though they may probably have been functionally seeds in the same sense as those of the Pteridosperms, are greatly inferior to the latter in morphological differentiation, and stand much nearer the Cryptogamic type of megasporangium. They are, in fact, the only really "primitive" seeds known to us, and as such are of special interest, though they probably only represent a side-line of evolution.

As regards the relation of the Palæozoic to the recent Lycopods, only the heterosporous forms of the latter come under consideration, for as yet we know nothing certain of the history of the homosporous Lycopodiaceae. It now seems clear that the genus *Selaginella*, or types scarcely distinguishable from it, already existed in the Palæozoic Flora, and that it had no near relation to the arborescent Lepidodendreae. On the other hand, there may well be some connection between the Lepidodendreae and the greatly reduced heterosporous genus *Isoëtes*, which, in the structure and insertion of its sporangia, as well as in anatomical characters, has much in common with the Palæozoic tree Lycopods. In the occurrence of sterile trabeculæ in the sporangia of some *Lepidostrobi*, Professor Bower has recognised an interesting point of agreement with *Isoëtes*.[1]

[1] The curious Triassic genus *Pleuromeia* has been regarded as a link between the two groups, but if, as is stated, the sporangia of *Pleuromeia*

The question of a possible relationship between the Palæozoic Lycopods and certain Seed-plants will be discussed when we come to the Gymnosperms.

PTEROPSIDA

The result of the palæobotanical research of the last twenty years has been to exalt the importance of the Fern phylum, which now appears to have been the source from which the great majority, if not the whole, of the Seed-plants were derived. At the same time the recent discoveries have greatly reduced our estimate of the actual number of the true Ferns in Palæozoic times (most of them having already become Seed-plants at that period), and difficulties have arisen in discriminating between the Ferns proper and their more advanced allies the Pteridosperms. Any certain knowledge of Palæozoic Filices is, for the moment, practically limited to the family Botryopterideae and a few other forms probably allied to them. We may follow Mr. Arber[1] in using the name Primofilices for the whole group. As regards the Marattiaceae, long considered as the dominant Ferns of the Carboniferous period, the question is much more difficult, as has been shown in Chapter VIII.

There is no reasonable doubt that the Botryopterideae were true Ferns; all their characters, both

were borne on the under side of the sporophyll, there is great difficulty in accepting this view. On *Pleuromeia* see Solms-Laubach, "Ueber das Genus *Pleuromeia*," *Bot. Zeitung*, Bd. lvii. 1899, p. 227; H. Fitting, "Sporen im Buntsandstein—die Makrosporen von *Pleuromeia*?" *Ber. d. Deutschen Bot. Gesellschaft*, Bd. xxv. 1907, p. 434.

[1] E. A. N. Arber, "On the Past History of the Ferns," *Ann. of Bot.* vol. xx. 1906, p. 221.

vegetative and reproductive, point in this direction, and the evidence has been materially strengthened by the observation of spores in process of germination, agreeing closely with corresponding early stages in the development of recent Fern prothalli (p. 339).

Anatomically, the Botryopterideae show two types of structure, the one (*Botryopteris* and its allies, p. 325) exceedingly simple as regards the stem-structure, while the other (*Zygopteris* and its allies, p. 306) shows a considerable degree of differentiation. The solid strand of tracheides, surrounded by phloëm, which constitutes the central cylinder in the *Botryopteris* group, is perhaps the simplest form of stele known in any Fern, but it would be rash to infer from this fact that these plants were necessarily of a specially primitive nature. Their roots are diarch, like those of most recent Ferns, their petioles attain some degree of complexity in vascular structure, while the differentiation of special fertile fronds indicates a rather high grade of organisation.

The affinities of the Botryopterideae with other Ferns have been fully discussed in Chapter IX., and the conclusion arrived at, that while they show some affinity with various Filicinean families of later origin, they cannot be considered as on the direct line of their descent. This line will have to be sought among other Primofilices, of which, as yet, we have only a scanty knowledge, though the occurrence of annulate sporangia on ordinary Fern pinnules, as in *Pteridotheca Williamsonii*, is a promising indication (p. 293).

Some relation between the Botryopterideae and the Ophioglossaceae was recognised by Renault when he first discovered the fossil family, the resemblances he

detected lying in the fructification and in the occurrence of reticulated tracheides. He regarded the Botryopteridеae as intermediate in stem and fructification between the Hymenophyllaceae, representing the Ferns properly so-called, and the distinct group Ophioglossaceae [1]—a view for which there is still much to be said. The sporangia of *Stauropteris* (a genus not known to Renault) present an almost exact agreement with those of *Botrychium*, as regards their structure and the mode of attachment by vascular pedicels.[2] The resemblance in the structure of the tracheides has proved to be even more striking than Renault was aware, for true pitted tracheides of a "Gymnospermous" type occur in both groups. It may be added that the structure of the stem in the new Botryopteridean genus *Botrychioxylon* (p. 318) if it lost the internal wood (a change likely to occur, from the analogy of parallel cases elsewhere [3]) would be almost exactly that of a *Botrychium*. The fact that the frond (at least the fertile frond) of certain Botryopterids branched in more than one plane has been compared with the dorsiventral branching of the frond characteristic of Ophioglossaceae.[4]

On the whole, a real affinity between the fossil and the recent family seems probable—in fact, of known plants, it is the Botryopterideae which appear to have most in common with the Ophioglossaceae.

Professor Bower thinks it "probable that the

[1] B. Renault, Végétaux silicifiés d'Autun, etc., Autun, 1878, p. 114.

[2] In *Botrychium* they are short, in this respect resembling those of *Botryopteris*.

[3] See below, p. 651.

[4] Lady Isabel Browne, "Phylogeny and Inter-relationships of Pteridophyta, vi. Filicales," *New Phytologist*, vol. vii. 1909, p. 27.

Ophioglossaceae sprang from some offshoot of the sporangiophoric Pteridophytes, allied in some degree to the Sphenophyllales,"[1] while he recognises an analogy with the Filicales. My own feeling is that the converse way of putting the relations is to be preferred. It appears probable that the Ophioglossaceae were derived from primitive Ferns, allied to the Botryopterideae, while they show analogies, in the way their sporangia are borne, with the sporangiophoric Pteridophytes, such as Sphenophyllales and Psilotales. On the view here adopted we should naturally regard the Ophioglossaceae with well-developed Fern-like leaves as, on the whole, the more primitive members of the family.[2]

All the evidence we possess as to the Ferns of early periods shows that they were already megaphyllous forms, comparable in habit to their later successors, and affords no ground for the supposition that they were derived from a microphyllous ancestry. It must, however, be admitted that our palæontological record for the Ferns (as for other Pteridophytic groups) is too short to settle questions of origin.

The majority of the Lower Carboniferous and Devonian Fern-like plants were probably Pteridosperms. It is as yet impossible to distinguish by the habit between these plants and the Ferns, and indeed the best proof we now have of the presence of true Ferns in Devonian rocks is the occurrence of petrified stems of *Asterochlaena* (p. 324).

[1] *Origin of a Land Flora*, p. 492.

[2] The evidence for saprophytic reduction within the family seems to be materially strengthened by the case of extreme reduction which has been found in *Ophioglossum simplex*. See, however, the views of Bower, *Origin of a Land Flora*, p. 477.

Though the Botryopterideae formed the basis of the group Primofilices, as proposed by Mr. Arber, some doubt has since been expressed whether this family really belonged to the Primofilices in the true sense of the word.[1] Miss Stopes points out that, since many of the Botryopterideae have tracheae with multiseriate bordered pits, like those of Gymnosperms, they are in this respect not absolutely true Ferns, but have taken one step towards Gymnosperm anatomy; the group therefore appears to contain members which are "Pro-Pteridosperms" rather than Primofilices pure and simple. The view has been taken here (p. 345) that the Botryopterideae are probably an offshoot from the same line of descent with the later Ferns, rather than their direct ancestors. They seem, however, to have been sufficiently near the original stock[2] to deserve in an eminent degree the name Primofilices, which does not necessarily imply direct ancestry. As regards the pitted tracheae, it appears probable that this form of water-conducting element was once common to the Fern phylum generally, but that the true Ferns have since for the most part lost it, adopting the very specialised scalariform type of vessel which is now characteristic of them (p. 314).

The question of the affinity of the Botryopterideae to the Pteridosperms is of great interest. The Pteridosperms

[1] M. C. Stopes, "A New Fern from the Coal-Measures, *Tubicaulis Sutcliffii*," *Mem. and Proc. Manchester Lit. and Phil. Soc.* vol. l. No. 10, 1906, p. 23.

[2] See especially the fine series of memoirs by Kidston and Gwynne-Vaughan on the fossil Osmundaceae, in which the close relations of this family with the Botryopterideae are demonstrated, *Trans. Royal Soc. Edinburgh*, vol. xlv. Part iii. p. 759, 1907; vol. xlvi. Part ii. p. 213, 1908; Part iii. p. 65, 1909.

sperms are so ancient that we can have no direct knowledge of their ancestry, but one naturally looks to the oldest known types of Ferns for indications of what it may have been.

It has been suggested that the more complex Botryopterideae, such as *Asterochlaena*, may have been related to polystelic types of Pteridosperms, such as *Medullosa*. A breaking up of the deeply lobed stele into separate meristeles is quite conceivable, and may well have led on to the structure of Cladoxyleae, in which the numerous steles tend to a radial arrangement (p. 497).[1] No light, however, is thus thrown on the history of the Medulloseae themselves, for, since the discovery of *Sutcliffia*, it seems clear that polystely arose within this Pteridospermous family, and was not derived as such from any ancestral stock.

It has already been pointed out that the Pteridosperms may probably have arisen from some early Fern-like type with a protostelic stem (pp. 464 and 473). In this respect, and in the structure of the tracheae, the simpler Botryopterideae may resemble the hypothetical ancestors of the Seed-plants, but there are not sufficient grounds for assuming any near relationship.

Professor F. W. Oliver's interesting discovery of a sporangium (*Tracheotheca*), similar to that of certain Botryopterideae, containing tracheides in the inner layers of its wall,[2] suggests an early approach to

[1] M. Paul Bertrand has quite recently come to the conclusion that *Clepsydropsis*, a Zygopteridean petiole, was borne on the stem of a *Cladoxylon*, "Sur les Stipes de *Clepsydropsis*," *Comptes Rendus*, Nov. 16, 1908.

[2] F. W. Oliver, "On a Vascular Sporangium from the Stephanian of Grand Croix," *New Phytologist*, vol. i. 1902, p. 60.

seed-structure, and may prove to be a valuable indication. At present, however, the case is too isolated for any phylogenetic conclusions to be drawn.

There can be little doubt that the Pteridosperms have some affinity with the Marattiaceae in the widest sense, though the connection between them may be indirect and impossible to trace accurately in the present state of our knowledge. We have already considered in some detail the evidence for the presence of Marattiaceae in the Carboniferous Flora (Chapter VIII.). The probability is decidedly in favour of their existence as a group of some importance at that time, though the question is by no means without difficulty (see p. 468). In any case the structure of the Pteridospermous male fructification *Crossotheca* (p. 396), and still more that of the stamens in the Mesozoic Bennettiteae (p. 586), indicates affinity between the older Seed-plants and Ferns of the Marattiaceous type, and heightens the probability that the latter are an ancient race. There are thus good grounds for the view expressed by Mr. Kidston that the Pteridosperms and Marattiaceae had a common origin. This hypothesis is not inconsistent with the idea of a relation between the Pteridosperms and the Botryopterideae, for, as we have seen, possible links between the latter family and Marattiaceae are to be found in *Corynepteris* and other genera (p. 344).

In the absence of any evidence of heterospory among Palæozoic Ferns, it appears that the gap between any known group of Ferns and the related Seed-plants must be a wide one. The general conclusion, however, that the Pteridosperms belonged to the

same phylum with the Ferns appears indisputable and needs no detailed proof. In all characters in which these early Seed-plants approach the Cryptogams, whether in habit, anatomical structure, the morphology of the sporophyll, or the nature of the microsporangiate fructification, it is with the Ferns alone that affinity is shown. The stock from which they were derived is still unknown, and may well have differed widely from any group of Ferns with which we are familiar, but there is no longer any room for doubt that it had far more in common with the Ferns than with any other race of Pteridophytes.

We have to conceive of the Pteridosperms as a vast plexus of varied forms, of which the few types as yet adequately known can give but a very imperfect idea. For example, we know nothing as yet of the structure of those Pteridosperms which, like *Aneimites* or *Pecopteris Pluckeneti* (pp. 465, 466), bore seeds of the bilateral type, resembling those of Cordaiteae. Our detailed knowledge is limited at present to the two series, Lyginodendreae (Chap. X.) and Neuropterideae (Chap. XI.), and even within these limits is very imperfect. The two families appear fairly distinct, as shown both by the vegetative and anatomical characters and by those of the seeds. Anatomically, the trend of evolution in the Lyginodendreae has been towards the elaboration of the single stele, in the Medulloseae (on the whole larger plants) towards the breaking up of the stele. The latter was an unprofitable course, ill adapted to the conditions of secondary growth, and it is probable that the polystelic line, after attaining an extreme elaboration,

became extinct about the close of the Palæozoic period.

In the series of the Lyginodendreae it appears evident that *Heterangium* represents, from an anatomical point of view, the most primitive stage known (p. 401). *Lyginodendron* itself is anatomically a *Heterangium* which has acquired a pith and isolated its leaf-traces.[1] It thus lies on the direct way to the stem-structure of the higher plants.

The view that the medullate stele of *Lyginodendron* was derived, by suppression of the central xylem, from the protostele of the *Heterangium* type is materially confirmed by the observations of Kidston and Gwynne-Vaughan on the fossil history of the Osmundaceae. In this analogous series they are led, by the investigation of various Permian Osmundaceae with tracheal tissue occupying the centre of the stele, to the conclusion that the pith of this family has been derived directly from an originally solid xylem mass.[2]

The Calamopityeae (p. 476) evidently form a parallel series to the Lyginodendreae; they are, perhaps, of even greater antiquity, and we have no light, as yet, on their derivation.

In later Palæozoic times we find, in the Cycadoxyleae (p. 483), plants which appear to have affinity with the Lyginodendreae, and may even have sprung from them.

[1] On the question of the anatomical evolution, my article on "The Old Wood and the New," *New Phytologist*, vol. i. 1902, p. 25, may be referred to.

[2] "On the Fossil Osmundaceae," Part iii. *Trans. Royal Soc. Edinburgh*, vol. xlvi. Part iii. 1909, p. 663. More direct evidence appears to be afforded by certain newly discovered stems of Lyginodendreae from the Moravian coal-balls (see below, p. 663) which further connect the structure of *Lyginodendron* with that of *Heterangium*.

These stems have taken an aberrant line of development, through the elaboration of anomalous secondary growth, and thus present some analogies with the more modified of the recent Cycadaceous stems. They may well have been Cycadophyta, though probably not closely allied to the known Mesozoic or recent types.

The relation of the Pteridosperms to the Cycadophyta is as clear as that to the Ferns, and indeed, as we have seen, it is often difficult to draw the line between the two first-named classes. For the present, it is convenient to keep the Pteridosperms distinct, on account of their relatively primitive character, but there is every reason to hope that further discoveries will effectually link them on to the typically Gymnospermous Cycadophyta. The anatomical resemblances, which led to the recognition of the Cycadofilices as a transitional group, have been immensely strengthened by the discovery of the seeds, which are sufficient in themselves to demonstrate a near affinity between the Pteridosperms and the Cycads. Curiously enough, the relation is closest with the seeds of the recent Cycadaceae, a group of which the geological history is still obscure. Those of the Mesozoic Bennettiteae are not so readily comparable, and evidently represent a more advanced stage of evolution, their seeds having been modified and in some respects simplified in correlation with the development of the complex fruit.

As regards the microsporangiate organs of the Pteridosperms, our present somewhat scanty information indicates that they were of the nature of synangia (p. 399); they thus find a remarkable analogy in the compound pollen-sacs of the Mesozoic Bennettiteae

(p. 586). The sporophylls, so little differentiated from the vegetative foliage, may best be compared with the stamens of Bennettiteae on the one hand, or with the foliaceous carpels of *Cycas* on the other.

The question whether the Lyginodendreae or the Medulloseae were the nearer to the main line of Cycadean evolution may be a sterile one, for there were doubtless many other races of Pteridosperms, among which the true ancestry may lie concealed. A few points of comparison may, however, be noted. So far as the anatomy of the stem is concerned, *Lyginodendron* appears to come near the Cycads, for the general organisation is of a similar character, and the mesarch structure of the bundles is still retained in the peduncles of the cones of some recent Cycads as well as in the leaves (p. 364). The habit and anatomy of the *Lyginodendron* foliage is, however, unlike anything known either in Mesozoic or recent Cycadophyta.[1] It has been suggested that *Lagenostoma*, the seed of *Lyginodendron*, may have given rise to the seed of Cycadaceae by the cupule becoming adherent to the integument, and thus constituting the supposed outer integument of the Cycadean ovule.[2] This view, however, assumes that the integument of the seed in recent Cycads is double, an interpretation which is still open to much doubt.

[1] It is conceivable that a reduction of a leaf of the *Sphenopteris* type might lead to a structure not unlike that of the leaf in the genus *Cycas*, with uninervate pinnæ. The very curious Annam species, *C. Micholitzii*, Dyer, with quadrifid pinnæ, is of interest from this point of view. See *Gardener's Chronicle*, August 19, 1905.

[2] Miss M. C. Stopes, "Beiträge z. Kenntnis der Fortpflanzungsorgane der Cycadeen," *Flora*, Bd. xciii. 1904; "On the Double Nature of the Cycadean Integument," *Ann. of Bot.* vol. xix. 1905.

Seeds of the *Trigonocarpus* type (p. 452), referable to Medulloseae, appear to have much in common with those of the Cycadaceae, as shown by the drupe-like differentiation of the testa, the double vascular system, and the form of the pollen-chamber. The chief difference lies in the free nucellus of the Trigonocarpeae, which contains the inner vascular system, whereas in the Cycadaceae the nucellus is adherent to the integument, and the inner vascular system is said to belong to the latter—a point exceedingly difficult to determine. In spite of these differences, I am inclined to regard the *Trigonocarpus* type as the nearest approach among Pteridosperms, so far as we know at present, to the seed of the Cycadaceae.

Anatomically, the Medullosean stem differs from that of recent or Mesozoic Cycadophyta in being polystelic (except in the protostelic *Sutcliffia*, which does not affect the question). Certain local peculiarities in the vascular system of various Cycads, due to anomalous distribution of the cambium, have recently been interpreted as relics of a polystelic structure, but these exceptional irregularities do not appear to bear more than a superficial resemblance to the primary polystely of the Medulloseae.[1]

On the other hand, the structure of the petiole and the organisation of the leaves generally are very similar in Medulloseae and Cycadaceae, and the resemblance

[1] Some of the most striking cases of so-called "polystely" among recent Cycads occur in the *root*, an organ which in the Medulloseae was monostelic. For the polystelic interpretation of Cycadean structure see Worsdell, "Structure and Origin of the Cycadaceae," *Ann. of Bot.* vol. xx. 1906, p. 129; Matte, *Récherches sur l'appareil libero-ligneux des Cycadacées*, 1903.

extends to the Bennettiteae of the Mesozoic. On the whole of the evidence available it appears likely that some at least of the Cycadophyta may have been derived from plants resembling the Medulloseae (Neuropterideae) in certain characters, though probably with monostelic rather than polystelic structure of the stem.

Leaving the Cycadophyta for the moment, we have now to consider the relation of the Pteridosperms to the Cordaitales, the characteristic Gymnosperms of the Palæozoic. In some respects two groups of plants could scarcely appear more different than the Fern-like Spermophyta and the typical Cordaiteae. In habit there is no resemblance, the Cordaitean trees having externally much more in common with Araucarian Conifers than with any of the known Pteridosperms (pp. 520, 522). The specialised cones or catkins of the Cordaiteae, grouped in inflorescences, are wholly remote from the compound, scarcely differentiated sporophylls, springing from the main stem, which bore the seeds and pollen-sacs in the Pteridosperms. The Cordaiteae are altogether on a far higher level of organisation, and deserve the place among true Gymnosperms which has always been assigned to them. But, though so advanced in structure, the family appears to be as ancient as any land-plants with which we are acquainted—a striking proof of the immense extent of evolution which had run its course before our palæontological record begins.

There are, however, clear proofs of affinity between Pteridosperms and Cordaitales, great as the differences between them appear. The strongest mark of affinity

is in the seeds, which are essentially of the same type in the two groups—in fact, it is impossible at present to point to any constant distinction between them. Of seeds already known in detail, the closest agreement is between the *Trigonocarpus* group and the Cordaiteae (pp. 452 and 546); they have in common the double vascular system, the drupe-like testa, the form of the pollen-chamber, and probably the free nucellus. On the other hand, they differ in the fact that the Trigonocarpeae are radiospermic, the Cordaiteae platyspermic, but this distinction has no general validity, for we have good evidence that bilateral as well as radial seeds occurred among the Pteridosperms (pp. 465 and 467).

Rhabdocarpus, attributed to *Poroxylon* by Grand'-Eury, only differs in small details from the seeds of Cordaiteae in the narrower sense (p. 512). We know nothing as yet of the seeds of the Pityeae, the third family making up our class Cordaitales.

As regards the anatomy, there is a very complete series leading from the stem of the Lyginodendreae to that of the typical Cordaiteae, as described by Renault. In *Calamopitys* we find the first signs of the dying out of the centripetal wood in the lower part of the leaf-trace bundle (p. 482). In *Poroxylon* the same condition recurs, with a general structure much like that of *Cordaites* itself (p. 506). In the Lower Coal-measures of England, stems otherwise indistinguishable from those of *Cordaites* have distinct remains of centripetal wood in the stem (p. 526). The Pityeae have likewise reduced and modified their primary xylem, perhaps in relation to a change of function (p. 515). The series

is not, of course, a chronological one, but it serves to link the stem of Pteridosperms of the Lyginodendreae type with that of true Cordaiteae ; it is at least an interesting point that the older Cordaitean stems generally show some trace of the centripetal wood, while it seems to have disappeared in the late Carboniferous or Permian species which Renault investigated. Concurrently with the gradual extinction of the old Cryptogamic wood, we find on the whole a tendency to greater density of the secondary wood, with a diminution in the width of the medullary rays. The double leaf-trace is a common, if not a constant, character at all stages, the division of the trace extending, on the whole, lower down into the stem in the later forms. Other details, such as the structure of the outer cortex, are also common to many members of the series, from the Devonian Calamopityeae to the Permian Cordaiteae. Without for a moment supposing that we have here the actual course of evolution before us, the series seems to afford as strong a proof as anatomical evidence is capable of affording that the Cordaiteae sprang from a Pteridospermous stock, while the leaf-structure supports this conclusion, the mesarch or exarch foliar bundles of Poroxyleae and Cordaiteae being a distinctly Pteridospermous character. On the evidence of the seed-structure and the anatomy together, the affinity of the Cordaitales with the Pteridosperms seems to be firmly established, though in point of time the connection must lie very far back.

The various Cycad-like characters which have long been remarked in both vegetative and reproductive organs of the Cordaiteae are doubtless to be explained, not

by any direct relation to the Cycads, but by common descent from an early Pteridospermous stock.

The Pteridospermous affinities of the Cordaiteae have an important bearing on the question of the systematic position of the Coniferae. It has generally been recognised that the Cordaiteae are related to the Coniferae, and if this be so, it follows that the latter are also ultimately of Pteridospermous descent, and thus belong to the great phylum of the Pteropsida.

Some authors, however, have endeavoured to derive the Conifers from the Lycopodiales,[1] while others have limited this theory to a portion only of the Coniferae,[2] implying that the order is an artificial assemblage, made up of at least two unrelated groups.

Of late the question has turned especially on the position of the Araucarieae, which Professor Seward has regarded as probably of Lycopodineous origin, while he leaves the question open for the rest of the Coniferae.[3] Some brief discussion of the question seems necessary here, as the issue involved is that of the single or multiple origin of the existing Spermophyta. The position of the Araucarieae will be primarily considered, since it is this group especially which is now in dispute.

[1] *E.g.* D. H. Campbell, *Lectures on the Evolution of Plants*, New York, 1899, pp. 166-167.

[2] *E.g.* H. Potonié, *Lehrbuch der Pflanzenpaläontologie*, Berlin, 1899, p. 320.

[3] A. C. Seward and S. O. Ford, "The Araucarieae, Recent and Extinct," *Phil. Trans. Royal Soc.* B, vol. 198, 1906, pp. 305-411. See also the "Report of a Discussion on the Origin of Gymnosperms at the Linnean Society," *New Phytologist*, vol. v. 1906, pp. 68 and 141, where the views of various botanists are briefly given.

The Araucarieae present a close agreement with the Cordaiteae in the structure of the stem, and especially in that of the wood, which, as universally admitted, is often indistinguishable in the two families. The essential feature is that the mass of the wood, apart from the medullary rays, is composed of tracheides with multiseriate bordered pits on their radial walls. This is the characteristic type of wood throughout the Cordaitales and Pteridosperms, extending also (in the form of primary xylem) to many of the older Ferns, while it is practically unknown among Lycopods,[1] in which the tracheides are very constantly scalariform. The absence of centripetal wood in the Araucarian stem presents no difficulty on the hypothesis of Cordaitean affinity, for its gradual disappearance in certain Pteridosperms and in the older Cordaitales can be traced, until it is lost in the stems of the typical Cordaiteae. No such links with the stem-structure of Lycopods are known.

The roots in Araucarieae (and Conifers generally) are essentially of the same type as in Cordaitales, and show none of the peculiarities of Lycopod roots.

The leaves of Araucarieae, with their numerous parallel bundles, agree generally, though not in detail, with those of Cordaiteae. That the multinervate character is primitive is indicated by the fact that the cotyledons likewise contain several bundles. Lycopods as a rule have only one foliar bundle, which, in the case of *Sigillariopsis*, divides into two. If the Araucarieae

[1] The only case I know of is in Renault's *Sigillariopsis Decaisnei*, where some of the tracheides are pitted, though they do not appear to agree at all closely with those of the Araucarieae.

are relatively primitive Conifers, a point on which I am disposed to agree with Professor Seward, it appears that the more complex type of leaf-structure is the original one for the Order. While the general anatomy of the leaf is thus entirely favourable to Cordaitean affinities, the histology lends no decided support to either view of the affinities. The vascular bundles have no typical centripetal wood, but are accompanied by transfusion-tissue, which we may either regard, with Mr. Worsdell and M. Bernard, as representing the centripetal xylem of Cordaiteae,[1] or may compare with the well-developed transfusion-tissue occurring in fossil Lycopods. On any view, the centripetal part of the xylem is a tissue which becomes modified or lost in the higher plants.[2]

Passing on to the organs of reproduction, the male cones of Araucarieae show some points in common with those of Cordaiteae. As we have seen, the stamens of the latter group have been well compared with those of *Ginkgo*. The stamens of Araucarieae, with their distally attached pollen-sacs, are of the same type as in *Ginkgo*, but the large number of the sacs brings them nearer to the Cordaitean stamen; on the other hand they differ absolutely from the sporophylls of the Lycopods, in which the constant relation of one sporangium to one sporophyll is a

[1] It will be remembered that, according to Miss Stopes's observations, transfusion-tissue, as well as centripetal xylem, occurs in the Cordaitean leaf (p. 534).

[2] The structure of Araucarian seedlings obviously cannot be used in the comparison with a fossil group. Recent work, however, shows that the anatomy of the seedling in Araucarieae conforms to the same type as that of the Cycadaceae and *Ginkgo*, while other Coniferae show a modification of the type in the direction of reduction.

character diagnostic of the class.[1] The numerous nuclei in the pollen-tube of the Araucarieae present a manifest analogy, as Professor Seward recognises, with the multicellular antheridia of Cordaiteae and Pteridosperms. At present we know nothing of the fertilisation of the "seed-bearing" Lycopods, so on this side the material for an equally close comparison is wanting.

The female cones of the Araucarieae alone appear to afford any real support to the Lycopod theory. The single ovule on the upper surface of the cone-scale offers an evident analogy with the sporangium and sporophyll of a Lycopod, though, if the Cretaceous *Protodammara*, with three ovules on each scale, is rightly referred to Araucarieae (p. 607), the value of the analogy becomes very doubtful. In any case the vascular system of the Araucarian cone-scale is totally different from anything in the sporophylls of Lycopods. The comparison between *Araucaria*, in particular, and *Lepidocarpon*, on which Professor Seward lays stress, appears to amount to no more than a distant analogy, for the part which envelopes the ovule in *Araucaria* is not, as in *Lepidocarpon*, the integument itself, but an extra covering enclosing an already integumented megasporangium.[2]

Until the nature of the so-called ligule, and, generally, the relation of the female cones of Araucarieae to those

[1] The comparison of the Araucarian stamen with the sporangiophore of *Cheirostrobus*, suggested by Professor Seward, is interesting, but by no means supports a relation to the Lycopods, with which *Cheirostrobus* can only have a remote affinity. The point is dealt with in the discussion on the "Origin of Gymnosperms" above referred to, pp. 143 and 147.

[2] See Figs. 25 and 26, p. 362 of Seward and Ford's *Araucarieae*.

of other Coniferae, are cleared up (which is far from being the case at present), it is useless to compare these strobili with fossil fructifications. It appears probable, however, that the comparison of the cone-scales with Lycopod sporophylls, though seductive, may be fallacious, the great complexity of the Araucarian cone-scale suggesting that the resemblance is limited to external characters.

The absence of a pollen-chamber in the Coniferous ovule is no doubt correlated with the abandonment of fertilisation by spermatozoids.

Without extending the discussion further, it may, I think, be concluded that the Araucarieae have many points in common with the Cordaitales, of sufficient weight to establish a real affinity, while the resemblances to the Lycopodineae are of a more doubtful and superficial nature, and appear to be completely outweighed by the great differences which separate these two groups.

Since the Araucarieae have been chosen as the family most favourable to the Lycopod theory of Coniferous descent, it does not seem necessary to discuss the question for the other families. The idea that the Coniferae include two wholly diverse groups, belonging to distinct phyla, appears to me quite untenable—either all are Lycopsida or all Pteropsida. The separatist view has arisen from paying attention too exclusively to particular organs rather than to the whole sum of characters. If any group could be regarded as distinct in origin from the rest it is the Taxaceae; even here it is only the morphology of the female fructification that presents any serious difficulties, and in this very point a

relation between the Podocarpeae (Taxaceae) and the Araucarieae has been traced, while the position of *Cephalotaxus* has oscillated between the Taxaceae and the Taxodieae, the latter being typical Pinoid Conifers.

Taking all the characters into account, there thus appears to be a decisive balance of evidence in favour of deriving the whole of the Coniferae from the Cordaitales, while not necessarily tracing them through the particular family Cordaiteae (of which, after all, our knowledge is still very narrow). The Conifers thus fall within the great division Pteropsida, though their connection with Ferns is obviously remote, a vast series of more or less primitive Spermophyta lying between. This view involves the conclusion that the microphyllous habit, which characterises so many of the Coniferae, is the result of reduction in the leaf, correlated with the increasing ramification of the stem, and also expressing a more perfect adaptation to the conditions of life on dry land.

The relations of the Ginkgoaceae to the Cycads and Cordaiteae are universally admitted, and need not be further discussed here (pp. 552, 612).

The characteristic Mesozoic Cycadophyta, the Bennettitales, were fully considered in the last chapter. Although the fossil Angiosperms do not fall within the scope of these "Studies," a few words may be added on the relation of the great modern sub-kingdom to the scarcely less dominant Cycadophyta of the Secondary Period.

The general arrangement of the organs in the Bennettitean fructification, as shown by Dr. Wieland's

classical investigations, is essentially the same as in a typical Angiospermous flower, with a central pistil, a surrounding whorl of stamens, and an enveloping perianth (see pp. 584, 585). The whole organisation, as Dr. Wieland at once recognised, is best compared with that of the flower in Magnoliaceae, such as the Tulip-tree (*Liriodendron*), while the resemblance extends to other orders of polypetalous Dicotyledons, *e.g.* Ranunculaceae and Nymphaeaceae. These groups, especially the Magnoliaceae, have been widely accepted as relatively primitive, and there is evidence for their occurrence in Cretaceous rocks.

As we have seen, the gynæcium of Bennettiteae shows some approach to the structure of a closed Angiospermous ovary, while the seed was practically exalbuminous, the large Dicotyledonous embryo filling the embryo-sac—a condition otherwise met with only among the Angiosperms.

Taking the whole of the characters into consideration, the evidence of affinity between the Mesozoic Cycadophyta and the Angiosperms appears very strong. It cannot, of course, be supposed that the Bennettiteae were on the direct line of Angiospermous descent, for there are manifest points of difference, notably in the great complexity of the stamens and in the organisation of the ovary-wall or pericarp, which was not formed by the carpels themselves, but by the associated sterile scales. There may be a difference of opinion as to the nearness of the relation between Bennettiteae and the higher Flowering Plants, but the points of agreement are so striking that we can hardly fail to recognise that a real relation exists, and that the ancestry of the

Angiosperms, hitherto the most obscure subject in the phylogeny of plants, is to be sought among the great plexus of Cycadophytes, which overspread the world during the Mesozoic Period.[1]

This conclusion opens up the question of the relation of Monocotyledons to Dicotyledons. If the Angiosperms were derived from Cycadophyta, it would appear to follow that the Dicotyledons were first evolved, for their structure has clearly much more in common with the Cycad type than that of the Monocotyledons. The latter would thus be regarded as a branch line of descent, diverging, no doubt at a very early stage, from the main Dicotyledonous stock. This view has been maintained, on other grounds, by various modern botanists. So far, however, as the palæontological record shows, the two classes are of almost equal antiquity, both appearing for the first time in Lower Cretaceous rocks. By the Upper Cretaceous age the Angiosperms had already seized the dominant position which they now hold; the Monocotyledons were always subordinate in numbers to the other class, but the occurrence of typical Palm-wood in Cretaceous rocks is a striking proof of the early evolution of one of the most characteristic Monocotyledonous families.

The relation of the Bennettiteae to the Pteridosperms, and through them to some early race of Ferns, has been sufficiently emphasised in preceding pages. We are thus led to the conclusion that the whole of the dominant sub-kingdom of Flowering Plants, if akin,

[1] See Arber and Parkin, "The Origin of Angiosperms," *Journal Linn. Soc.* (*Bot.*), vol. xxxviii. 1907.

as we believe, to the Cycadophyta, belongs ultimately to the phylum which takes its name from the Ferns. We may add that the Gymnosperms, as a whole, may be referred to the same stock, for evidence has recently been adduced that the small group of the Gnetales (the only outstanding Gymnospermous family) may have been derived, by reduction of the floral organs, from forms allied to the Bennettitales.[1]

It thus appears, if the views here taken are justified, that the whole of the Spermophyta, whether Angiospermous or Gymnospermous, were ultimately derived, through primitive Seed-plants of the nature of Pteridosperms, from the same stock with the Ferns. With this far-reaching conclusion we may conclude our consideration of the phylogenetic results of our studies.

In bringing these "Studies" to a close, it is well to recall the necessary limitations of all attempts to unravel the past history of organisms. Our ideas of the course of descent must of necessity be diagrammatic; the process, as it actually went on, during ages of inconceivable duration, was doubtless infinitely too complex for the mind to grasp, even were the whole evidence lying open before us. We see an illustration, on a small scale, of the complexity of the problem, in the case of domesticated forms, evolved under the influence of man. Though we know that our cultivated plants, for instance, have been developed from wild species within the human period, and often within quite recent years,

[1] Arber and Parkin, "Relationship of the Angiosperms to the Gnetales," *Annals of Botany*, vol. xxii. 1908.

yet nothing is more difficult than to trace, in any given instance, the true history of a field-crop or a garden plant, or even, in many cases, to fix its origin with certainty. In the history of natural groups, where the geological record takes the place of the cultivator's notes, the problem increases so immeasurably in difficulty, that a full solution becomes impossible.

But although, in endeavouring to form an idea of the course of evolution of any part of the Vegetable Kingdom, we can only hope, at the best, to construct a scheme, representing in a much simplified form the real succession of events, we must take care not to be misled by our own constructions. We must remember that, at all periods, competition among living things was as keen as now, and that in every age all the available places must soon have been filled. Hence, even in the earliest times of which the palæontologist take cognisance, there must always have been specialised forms, and even what we call "synthetic" types were themselves specialised to suit some particular set of conditions. Thus, at every step in the investigation of the fossil evidence, the same caution in distinguishing between the newer and the older characters is demanded, as when we are dealing with recent organisms.

Yet, in spite of these difficulties, and others, more obvious, which will at once occur to the mind, there can be no question that the study of the actual records of the past is of inestimable value in attacking a problem which is in its essence an historical one.

In these "Studies" the fossil record has been considered almost wholly from a morphological and evolutionary

point of view. There is room, even with the material already available,[1] for important work on other lines. The subject of the biology and ecology of fossil plants, as illustrated especially by their physiological anatomy when suitably preserved, offers a wide and promising field of research. Such biological studies will be of the greatest intrinsic interest, and will also throw a new and welcome light on the problems of Evolution.

[1] New sources of material, especially of petrified specimens showing structure, are urgently to be desired. As this book goes to press, I have received from Dr. Kubart of Graz sections from the magnificently preserved nodules of the Moravian Coal-measures, a field hitherto unworked from a structural point of view.

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